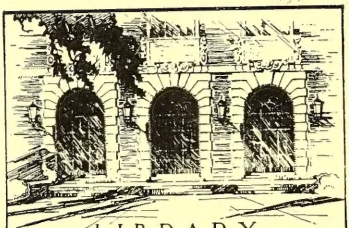
LIBRARY
OF THE
UNIVERSITY
OF ILLINOIS
570.5
ILL
v.20
cop. 2

The person charging this material is responsible for its return on or before the **Latest Date** stamped below.

Theft, mutilation, and underlining of books are reasons for disciplinary action and may result in dismissal from the University.

University of Illinois Library

JUN 24 1969

OCT 27 1986

MAY 16 1986

OCT 12 2007

L161—O-1096

Digitized by the Internet Archive
in 2011 with funding from
University of Illinois Urbana-Champaign

http://www.archive.org/details/minimumareasford203vest

JAN 31 1951

MINIMUM AREAS FOR DIFFERENT VEGETATIONS

Their Determination from Species-Area Curves

BY

ARTHUR G. VESTAL
The University of Illinois
Department of Botany

NAT. HIST.

UNIVERSITY OF ILLINOIS PRESS: URBANA
1949

ILLINOIS BIOLOGICAL MONOGRAPHS is a general title comprehending a series of monographs on subjects in botany, entomology, zoology, and allied fields. Each issue is an independent publication. For the convenience of bibliographers and librarians, each year's output is called a volume. Each volume consists of approximately 450 pages, priced at four dollars. A volume may consist of two, three, or four individual monographs. Prices of individual numbers are indicated in the list of titles given below. Requests for exchanges should be addressed to the Exchange Department, University of Illinois Library, Urbana, Illinois. All communications concerning sale or subscription should be addressed to the Director, University of Illinois Press, Urbana, Illinois.

Vol. I

Nos. 1-2. A Revision of the Cestode Family Proteocephalidae. With 16 plates. By G. R. La Rue. $2.00.
No. 3. Studies on the Cestode Family Anoplocephalidae. With 6 plates. By H. Douthitt. 80 cts.
No. 4. Some North American Larval Trematodes. With 8 plates. By W. W. Cort. $1.20.

Vol. II

No. 1. Classification of Lepidopterous Larvae. With 10 plates. By S. B. Fracker. $1.50.
No. 2. On the Osteology of Some of the Loricati. With 5 plates. By J. E. Gutberlet. 50 cts.
No. 3. Studies on Gregarines. With 15 plates. By Minnie E. Watson. $2.00.
No. 4. The Genus Meliola in Porto Rico. With 5 plates. By F. L. Stevens. (*Out of print*).

Vol. III

No. 1. Studies on the Factors Controlling the Rate of Regeneration. By C. Zeleny. $1.25.
No. 2. The Head-capsule and Mouth-parts of Diptera. With 25 plates. By A. Peterson. $2.00.
No. 3. Studies on North American Polystomidae, Aspidogastridae, and Paramphistomidae. With 11 plates. By H. W. Stunkard. $1.25.
No. 4. Color and Color-pattern Mechanism of Tiger Beetles. With 29 black and 3 colored plates. By V. E. Shelford. $2.00.

Vol. IV

No. 1. Life History Studies on Montana Trematodes. With 9 plates. By E. C. Faust. $2.00.
No. 2. The Goldfish (*Carassius carassius*) as a Test Animal in the Study of Toxicity. By E. B. Powers. $1.00.
No. 3. Morphology and Biology of Some Turbellaria from the Mississippi Basin. With 3 plates. By Ruth Higley. $1.25.
No. 4. North American Pseudophyllidean Cestodes from Fishes. With 13 plates. By A. R. Cooper. $2.00.

Vol. V

No. 1. The Skull of Amiurus. With 8 plates. By J. E. Kindred. $1.25.
No. 2. Contributions to the Life Histories of *Gordius robustus* Leidy and *Paragordius varius* (Leidy). With 21 plates. By H. G. May. $1.50.
Nos. 3-4. Studies on Myxosporidia. A Synopsis of Genera and Species of Myxosporidia. With 25 plates and 2 text-figures. By R. Kudo. $3.00.

Vol. VI

No. 1. The Nasal Organ in Amphibia. With 10 plates. By G. M. Higgins. $1.00.
Nos. 2-3. Revision of the North American and West Indian Species of Cuscuta. With 13 plates. By T. G. Yuncker. $2.00.
No. 4. The Larvae of the Coccinellidae. With 6 plates. By J. H. Gage. 75 cts.

[*Continued inside back cover.*]

ILLINOIS BIOLOGICAL MONOGRAPHS

VOLUME XX, NUMBER 3

PUBLISHED BY THE UNIVERSITY OF ILLINOIS AT URBANA
UNDER THE AUSPICES OF THE GRADUATE COLLEGE

EDITORIAL COMMITTEE

HARLEY JONES VAN CLEAVE
WILLIAM R. HORSFALL
LELAND SHANOR

MINIMUM AREAS FOR DIFFERENT VEGETATIONS

Their Determination from Species-Area Curves

BY

ARTHUR G. VESTAL
The University of Illinois
Department of Botany

UNIVERSITY OF ILLINOIS PRESS: URBANA
1949

Copyright, 1949, by the University of Illinois Press. All rights reserved. Permission for reproduction in any form may be obtained from the publisher.

MANUFACTURED IN THE UNITED STATES OF AMERICA

CONTENTS

INTRODUCTION 1

DEVELOPMENT OF THE METHOD 2

CONVERSION OF DATA TO SERVE AS BASIS FOR CURVES

From nominal to effective plot-size 7
From separated plots to one-piece equivalent area 7
From F% to average number of species per plot 8
From larger or smaller tree-diameter-limit to three-inch limit . . 9
Change of species-number for changed number of individuals . . . 10
Analysis of plot-maps, and random spotting 10

RELATION OF FISHER'S SERIES TO SPECIES-AREA PROBLEMS 13

RESULTS: REFERENCE AREAS AND THEIR SPECIES-NUMBERS

Trees of old-growth mixed deciduous forests 18
Other deciduous forests 21
Northern pine forests 21
Sclerophyll oak woodland 22
Subtropical forests, and low-latitude mountain forests 23
Tropical forests: Philippines, Borneo, Singapore, Ceylon 25
Tropical forests: West Africa 28
Tropical forests: South America 33
Subtropical thicket and heath, Mauritius 36
Chaparral and bush, California 37
Mediterranean shrub vegetation 40
North-European heath and dwarf-shrub vegetation 42
Shrub and bush of Rocky Mountains and Great Basin 45
Grasslands: tall-grass prairies, and sand prairie 48
Grasslands of Great Plains and mountain border 54
Mountain and intermont grasslands, Colorado 56
Columbia Basin grasslands 57
Desert grassland, southeastern Arizona 60
Grasslands in Europe: Switzerland 61
Grasslands: Denmark, Esthonia, Poland, Russia 64
Tropical secondary grassland 66
Ground cover of forests: bracken–blueberry type, Michigan . . . 66
Herbaceous ground-cover under forest 69
Dwarf-shrub ground-cover of boreal forests. 73
Ground vegetation within tropical forests 75
Bog vegetation 76
Lichen and herbaceous vegetation of rocky surfaces 80
Stratified and mixed communities and complexes 86
Scattered conifers + shrub + grass 87

Strata in mixed deciduous forest 89
Strata in conifer forest 90
Three-layered raised bogs, central Russia 92
Bush + grass 95
Desert shrub + ephemerals 99
Animal assemblages: sea-bottom, forest-soil Apterygota, stream fishes 101
REVIEW OF SPECIES-AREA FINDINGS
Magnitude and range of reference areas for different types . . . 106
The geometry of S-curves 110
Factors influencing the size of reference areas 112
Implications of certain results 116
Hypotheses to explain species-area curves 118
Additional studies needed 120
BIBLIOGRAPHY 122

INTRODUCTION

MANY STUDIES in ecology, agronomy, forestry, and range management have been made upon sizes, numbers, and arrangements of plots and study-areas of vegetation. Interest has commonly centered upon ecological or statistical method, or even more frequently upon economy of sampling. In this paper, emphasis is chiefly upon extent and the concomitant variation in number of species both as a phenomenon of vegetation and as an important characteristic by which different communities or different stands may be compared. A simple and widely applicable means of making such comparisons is offered, with results of applying it to about 240 examples of vegetation in many parts of the world. Briefly, the method is to use data for different-sized areas in a community to construct an S-shaped species-area curve on semi-logarithmic paper. The second step is to locate upon this curve two "reference areas," by means of conventionally adopted ratios of one to the other, as to both extent and number of species. A particular reference area of one vegetation is considered to be equivalent, in at least certain respects, to the same reference area of any other vegetation.

The writer is indebted, for use of data and for other cooperation, to officers of the California Forest and Range Experiment Station, particularly to Jerome S. Horton of its Glendora office; and for mathematical guidance to Dr. Paul B. Johnson of Occidental College, for a time at the Glendora office. During later stages, Dr. E. L. Welker, University of Illinois, more recently statistician for the American Medical Association, was mathematical adviser. Dr. John E. Potzger, Butler University, has furnished detailed plot data for numerous forests. The figures were drawn by Professor John E. Pearson, University of Illinois. The writer is very grateful for these substantial aids.

DEVELOPMENT OF THE METHOD

The curves first used were drawn to linear co-ordinates; later, number of species was plotted against logarithm of area. Semi-logarithmic paper is convenient for this purpose. After a number of trials, the hypothesis at first followed, that species-number varies directly with log of area, and that the curve consequently should be a straight line, was found to be untenable. All communities necessarily yield a curve which is concave in its lower or small-area section. Communities with data for sufficiently large areas, so far as studied, show a convex upper section, indicating a decline in species-increment from the logarithmic rate. Facts which presumably account for this decline will be given later. The curve thus has an S-form.

The difficult problem with a species-area curve has been to locate upon it one or more definite and strategic points or stopping-places which can be identified with certainty. If an area can thus be identified, it can serve as an effective plot-size, or as a larger study-area which will surely include all important species and a sufficient number of the less common species, including those especially characteristic of the type. The several proposals thus far made toward this problem have proved illusory. They give different results if the scale of one of the two variables is altered, or if they depend upon an accidentally determined largest area studied in the field. The problem is perhaps insoluble, but practical utilization of species-area curves to determine what are called reference areas is not difficult. A reference area is one yielding a definable degree of information concerning the stand or type in which it lies. It can be determined by several means of intensive study within a particular vegetation. Connections between numbers of species and degrees of informativeness have been found for several sizes of reference area in a study of trees in two old-growth mixed forests in Illinois by Vestal and Heermans (1945). They learned (p. 129) that the plot-size with half as many species as in a fair-sized stand was the same as that which qualified as the "smallest representative area," and that (p. 130) an area five times the small one, "large enough to include all important species and nearly half of the minor species, should be large enough to show many characteristics of the type." This intermediate area clearly identifies the type of forest; it provides a minimum statement of composition with approximate ranking of species as to number of trees and as to some measure of bulk or of ground-space occupied. It is called "minimum area for assignment to type," or briefly "minimum area." It is too small to give a dependable picture of diameter-distribution (form of stand). The "fair-sized stand" mentioned, a third reference area, is 50 $\times$ the smallest representative area, 10 $\times$ the minimum area.

If these different-sized pieces of one vegetation show definite ratios of species-number with particular area ratios, is it likely that similar relations will hold for other vegetations? The question seemed to deserve a test. Given certain field

data, it should be possible to determine actual values of reference areas for almost any vegetation, since their relative values are defined in terms of one another; i. e., the smallest representative area is that size which, having one-fiftieth the extent of another, includes half as many species. As a concrete example, we may ask whether the 136 milacres identified as the smallest representative area for a pine forest in Wisconsin is equivalent (i.e., comparable in many respects) to the 803 milacres found in the deciduous Brownfield Woods in Illinois. There are strong indications that they are equivalent. For this pine forest and for many other communities studied it is evident that all of the principal species are included in the smallest reference area. More detailed evidence is not yet sufficient to tell how close the equivalence may be. It can be said after trials with many kinds of vegetation that the results appear to be consistent with one another, and with the described characteristics of the different kinds of plant cover treated.

Restating the hypothesis: It is proposed that reference areas be defined in terms of ratios of area and of number of species, the conventional ratios adopted being those found after intensive study in one particular forest; and that reference areas so identified for different kinds of vegetation are presumably equivalent to one another in many respects, chiefly as to degree of informativeness.

While on a species-area curve no one strategic point can be singled out, any two points related to each other by predetermined ratios such as 1 : 50 for area and 1 : 2 for species-number, can be fixed upon with certainty. This possibility occurred to the author during the summer of 1944 while studying species and area in chaparral communities, and while the graphs were being drawn as sloping straight lines. The problem was submitted for mathematical scrutiny to Mr. Paul B. Johnson, statistician, then at Glendora, California.

He quickly proved that the two points were readily determinable, and resolved the problem into a simple case of two linear equations with two unknowns, having a unique solution. Fig. 1 illustrates the problem of locating two reference areas, Ar and Af, on a straight-line graph. Numbers of species at these areas are respectively Sr and Sf. (The "r" signifies smallest representative area, "f" is for fair-sized stand.)

The sloping line, drawn through points representing particular species numbers at particular areas, is the species-area graph. Locations of Ar and Af are to be determined. Two constants incidental to the problem are a, number of species at unit area, and b, the slope or pitch of the graph. Mr. Johnson has kindly furnished the following compact algebraic statement. It is in general terms, applicable to any species-number and area ratios which might be adopted, with the addition (in brackets) of quantities dependent on the particular ratios here used:

$$\text{The significant ratios are: } \frac{\text{Af}}{\text{Ar}} = r \ [= 50],$$

$$\text{and, } \frac{\text{Sf}}{\text{Sr}} = v \ [= 2].$$

The required values are: $\mathrm{Sr} = \frac{b \log r}{v - 1}$ $\left[= \frac{b \log 50}{1} \right]$.

$\mathrm{Ar} = \text{antilog } \frac{\mathrm{Sr} - a}{b}$.

$\mathrm{Sf} = v\ \mathrm{Sr}$ [$= 2\ \mathrm{Sr}$].

$\mathrm{Af} = r\ \mathrm{Ar}$ [$= 50\ \mathrm{Ar}$].

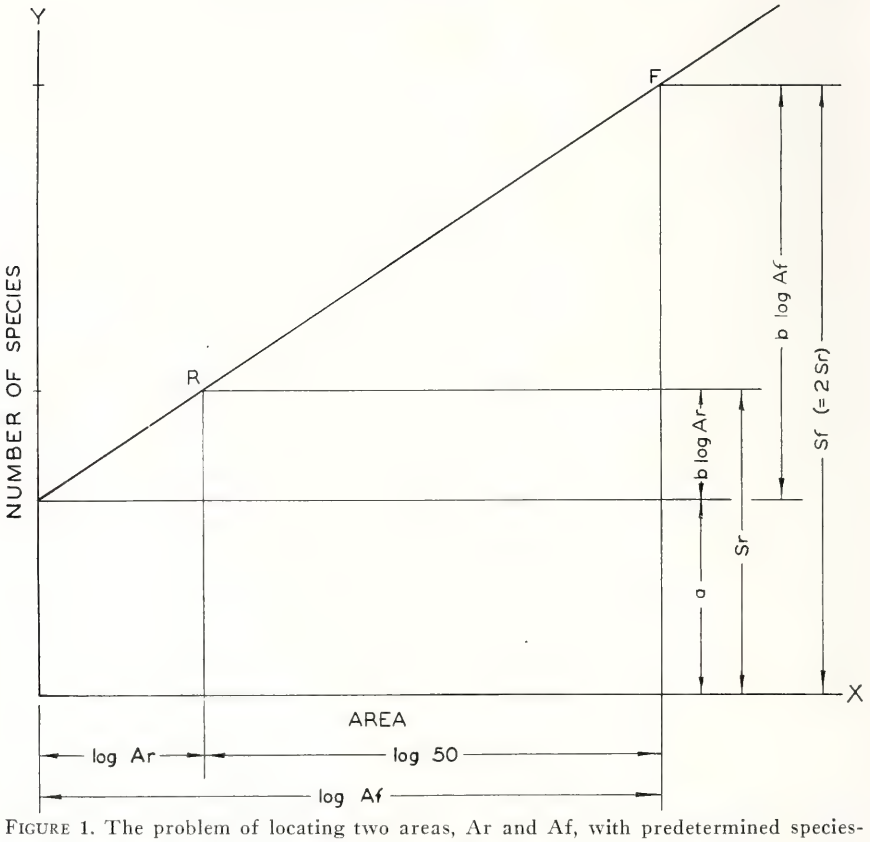

FIGURE 1. The problem of locating two areas, Ar and Af, with predetermined species-number and size ratios on a species-area graph assumed to be a straight line. See text.

A trial-and-error method of locating Ar and Af is simpler and quicker than the algebraic solution, and unlike the latter, can be used on S-curves. One puts on a slip of paper two marks separated by an interval representing a fifty-fold increase of area on the logarithmic scale used. First one judges visually the approximate levels for the two points, the upper being twice as high above zero species as the lower. Then, with the left-hand mark on the curve at the presumed lower point, or "trial Ar," one reads species-numbers for the two points. If the species-number read at the presumed Af is less than twice the other, the trial areas are larger than need be; if more than twice, smaller. Shifting in the proper direction, one writes down species-numbers for one pair of areas slightly upslope, and for another pair slightly down-slope, of the true but still unknown positions. Then the exact values are found by interpolation. In the following

example, C is the computed Sf, $= 2 \times S$ at trial Ar; G is the species-number read from the graph at the presumed Af; and d's are differences.

It will be recalled that a reference area of intermediate size, minimum area or

Computation from S-curve
for Kenoyer's *Chamaedaphne* bog near Kalamazoo

	Trial Ar *milacres*	S at Ar	Af, = 50 Ar *milacres*	C	G	$C - G$
	2.2	15.30	110	30.60	30.36	+0.24
	2.1	15.10	105	30.20	30.23	—0.03
d's	.10	.20	5.0	.40	.13	.27
d's × 3/27	.011	.022	0.555	.044	.014	
	2.11	15.12	105.55	30.24	30.24	
	Ar	Sr	Af	Sf		

Am, has been mentioned. It is perhaps more significant than either Ar or Af. It is found, after the other two are known, from its conventionally defined area ratio, 5 × Ar. It occurs, in all instances thus far determined, on the convex part of the curve. Since degree of convexity and beginning place of convexity vary for different communities, the corresponding species number, Sm, is best read from the curve at Am. The ratio of Sm to Sr, if the straight-line logarithmic

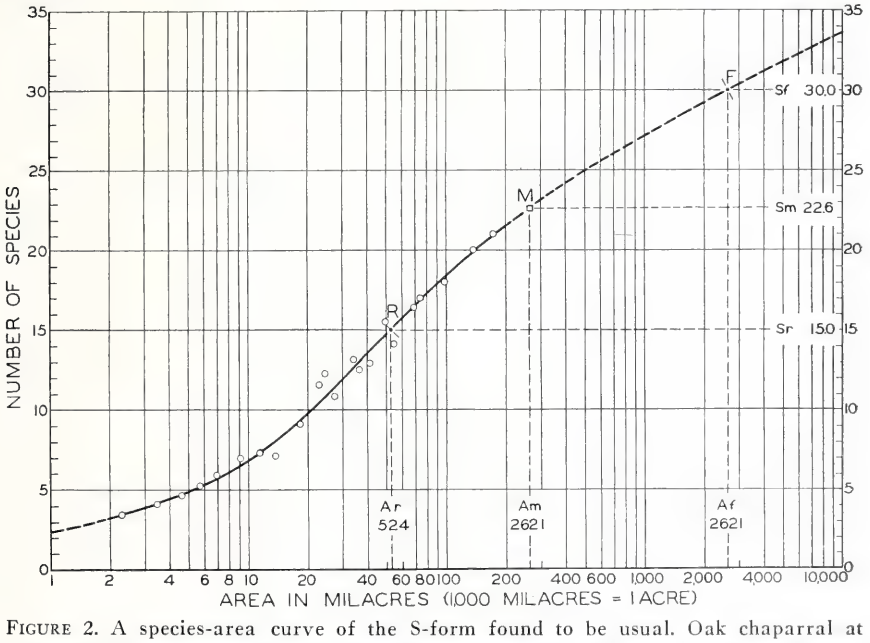

FIGURE 2. A species-area curve of the S-form found to be usual. Oak chaparral at Tanbark Erosion Plots, San Gabriel Range. Data from California Forest and Range Experiment Station. Four leading species. Plot-area basis is 173 milacres, with 21 species. Reference areas are large, since four shrubs, especially *Quercus dumosa* and *Ceanothus crassifolius*, dominate so strongly that little room is left for other species. The marked reference points R, M, and F, identify Ar (smallest representative area) at 52.4 milacres, with 15 species; Am (minimum area) at 262 milacres (1060 sq. m.), with 22.6 species; and Af (fair-sized stand) at 2621 milacres, with 30 species.

graph were the true form for species-area curves, would be a constant, 1.4114. On S-curves it is greater than this, usually between 1.44 and 1.5. In fig. 2 the three reference points are marked upon the curve.

If Sm : Sr were a constant ratio, it would be simpler to locate the two smaller reference areas on the curve, ignoring Af. Because of variations in the form of the curve, because a greater degree of accuracy is attainable with the greater spread of area, and because of a complication which may in a few cases be encountered, it has seemed greatly preferable to use Ar and Af as the areas to be first determined.

The complication, first pointed out by Mr. Johnson, is that on an S-curve there may be *two* pairs of areas which will satisfy both the area and the species-number ratios. One pair is very much smaller than the other, and is located on the concave lower section of the curve. Most sets of species-area data do not include such small areas, and the small pair of spurious reference areas consequently does not appear on most curves.

If they are encountered, there should be no difficulty in recognizing them from their position on a concavity, and from their usually obviously inadequate degree of inclusiveness. There are a few instances in the literature, of species-area data from which extremely small minimum areas were inferred. The curves were plotted to linear coordinates from a very small range of plot sizes, and did give the appearance of adequacy to the less-meager sizes studied. If the curve is drawn with logarithmic area scale, over a sufficient range of sizes, this kind of inference will not be made. The false reference areas will appear less frequently, and will be farther from the real reference areas if the two sizes adopted are separated by a 50-fold area-spread rather than by a 5-fold spread.

Certain floristically-poor communities have at first appeared to give S-curves which fail to include on any part of them a two-fold species increment in a 50-fold increase of area. Those thus far met with do not afford adequate species-area data to demonstrate that this is real; yet it may be so. If so, some other standard must be adopted for such communities, such as the use of an Sf : Sr ratio smaller than 2, say 1.7, or use of Am : Ar and Sm : Sr ratios only. The rather scanty data for the floristically-poor communities studied lend themselves to construction of curves which do give a 2-fold increment.

Mr. Johnson has suggested that if or when a sufficient degree of dependability and precision in the obtaining of field data and construction of S-curves permits a better understanding of their properties, it may be possible to recognize a strategic point from the form of the curve itself. He looks for such potential significance to the point of inflection (or "flex point"), at which the change from concavity to convexity takes place. At present the curves cannot be drawn with sufficient degree of certainty to know just where the flex point should be. The geometric determination of a significant area is thus not yet feasible. Yet it may be noted that the small reference area, Ar, is usually near, or not far above, the flex point (see Fig. 2).

CONVERSION OF DATA TO SERVE AS BASIS FOR CURVES

(Readers interested only in results may omit this section.)

Since regrettably few sets of plot data are published in full, and since the methods and objects of obtaining them vary so greatly, it was necessary to modify much that is usable in published or otherwise accessible material, adapting it to the present end of constructing species-area curves. For this reason many curves made for this study are from too scanty or uncertain figures, and reservations are stated along with the results. Much that is available and of great promise has had to be left unworked.

FROM NOMINAL TO EFFECTIVE PLOT-SIZE

The practise of Raunkiaer (1909-10) and of some users of his method (Vahl, 1913, Ramaley, 1942) has been to count as included within the small plot-size of 0.1 square meter all plants whose crowns extend over any part of the plot. Effective plot-size is thus greater than stated area, and is greater for plants with larger crown-spread. Raunkiaer plots are usually arranged along one straight line, and are well separated at uniform interval in any one set of 50 .1-sq.-m. plots. Such plots are difficult to compare with contiguous plots, usually larger, in which rooted shoots must usually be present to be counted. Contiguous plots are more amenable to species-area study. For each set of separated small plots of the Raunkiaer type an independent judgment must be made to estimate a likely plot size. Usual estimates are 2 to 4 $\times$ nominal plot size. In an extreme case, Ramaley's sagebrush in the San Luis Valley of southern Colorado (1942: Table 8), his additional statements of plant-size and open spacing enable one to infer that the 210 bushes recorded in his 200 0.1-sq.-m. plots are as many as would normally be found in 61.8 milacres. The effective plot size is estimated to be 0.309 milacres or 1.25 sq. m.; 12.5 times the nominal plot area.

Du Rietz has also followed Raunkiaer's convention of including plants which overlap from outside; he has used many plot-sizes; for his *Pinus–Calluna* at Sandön (1921: 153), 0.01 to 16 sq. m. For this the conversions used are: nominal .01 sq. m. to effective .03 milacre; .04 sq. m. to .06 mlc.; .25 sq. m. to .2 mlc.; 1 sq. m. to .3 mlc.*

FROM SEPARATED PLOTS TO ONE-PIECE EQUIVALENT AREA

A distinction is made between a sizable unit of vegetation in one piece and of compact shape, and the more commonly studied group of separated plots or

* "Mlc." is used as a coined abbreviation for milacre: the unit of area found generally convenient. It equals 43.56 sq. ft. Milacre plots, 6.6 feet on a side, are commonly used by American foresters for tree seedlings. Such a plot is a little over 4 square meters (4.04687). Multiplying number of milacres by 4 gives fair approximation to metric areas. One square meter equals 0.2471046 milacres. In the section giving results from curves, minimum areas are stated in square meters as well as in milacres.

strips having the same aggregate area. Not all characteristics of the one-piece unit are the same as those of the aggregate. The latter is generally used because it provides a larger assortment of species and a more inclusive sample of the always-present variations in both site conditions and plant cover. In this understandable striving for economy, certain features and individualities of the one-piece areas in sizes larger than the usual plots may have been overlooked. Since a point on a species-area curve represents an integral area, estimates converted from plot-aggregates are required. This is one of the greatest difficulties encountered. Fortunately a standard was at hand for aid in estimating equivalents for groups of 100-sq.-m. tree plots, many of which were contributed by Potzger and Friesner and their associates, notably Scott McCoy. This standard is a grid of 64 contiguous tenth-acre tree plots, completely mapped, from Trelease Woods near Urbana, Ill., one of the two forests studied intensively. The one-piece areas required were to be equivalent to alternate-plot strips of varying length (plots enumerated alternating with blank areas of equal size). From the grid were selected strips of alternate plots of fortieth-acre size (just larger than 100-sq.-m. plots). Their species-numbers were counted for varying lengths of strip, one-piece areas giving these numbers of species were found from the species-area curve for the grid, and results were put together in a simple graph. From this graph, multipliers were found which give approximate one-piece equivalents for a considerable variety of separated-plot combinations. Thus:

Equivalents for Alternate-Plot Strips of 25-Milacre Tree Plots

No. of plots in strips	5	10	15	20	25	40	50
Equivalent one-piece area (in plot units)	5.5	12.2	20.2	29.6	40	68	86.5
Multiplier	1.1	1.22	1.35	1.48	1.6	1.7	1.73

The larger a plot-size (considering also the size of plants in the vegetation studied) the smaller is the multiplier to be used. The more remotely plots are separated, the larger the multiplier. One long line of plots samples a larger area than the same number of plots (with the same interval between plots), arranged in several parallel lines. From such considerations judgments were made of one-piece areas equivalent to the various groupings of plots in the data available from many sources. The total area equivalent to a grouping of 50 small plots in one long line (the Raunkiaer plan) was taken to be $1.73 \times 50 \times$ the effective plot-size used.

FROM F% OR FREQUENCE OF OCCURRENCE IN PLOTS, TO AVERAGE NUMBER OF SPECIES PER PLOT

Many enumerations of plot-aggregates fail to give details for individual plots, or to state the average number of species per plot. If, however, the statement includes number or percentage of plots in which each species occurs, and if the species are completely listed, it is simple to compute species per plot. In a sense, frequence and species-per-plot bear inverse relation to each other. One tells

about species in terms of plots, the other about plots in terms of species. To find species-per-plot, consider each occurrence of one or more individuals of one species in one plot to constitute one "occurrence." The total of occurrences for one species is the number of plots in which it occurs. Add the occurrences for all the species to get total of occurrences. (This total appears as the number of "points" in many of Raunkiaer's columns for particular lines of 50 plots.) Divide total occurrences by number of plots in the aggregate. The quotient is the average number of occurrences per plot, which is the same as average number of species per plot. If proof is needed, try it on any known set of data.

It makes no difference whether plots are scattered or contiguous: the quotient is the correct average species-number for the plot-size or the effective plot-size.

While a series of species-numbers from which a curve is made is expected to come from a single stand, yet it may in certain instances be permitted to combine data from different stands not too unlike and within the same district. This makes possible a use of data such as those of Du Rietz, Fries, Osvald, and Tengwall (1920), and of Du Rietz (1921) for vegetation in northern Europe. In such cases, if no statement is given of species-per-plot, the given constance percentages can be used to determine average number of occurrences per plot in exactly the manner described for frequency. If the curve is a composite from different stands, that fact should be specified.

FROM LARGER OR SMALLER TREE-DIAMETER-LIMIT TO THREE-INCH LIMIT

It is not possible to compare different forests if the lower limit of size of trees included is appreciably different. For different reasons the limit actually used varies widely. Conversion to the same limit is much easier if given data include trees smaller than the limit adopted, since it is safer to exclude than to extrapolate. The limit here used is three inches (7.72 cm.) at breast height. This is not greatly different from either the 7-cm. or the 10-cm. limit commonly used.

Various expedients have been used to convert number of trees per acre from one limit to another. Some of the Philippine forest examples (and others in the tropics) enumerate small trees in small plots by height-classes, and larger trees in larger plots by diameter-classes. A few tables listing trees in the same plots by both types of size-class permitted the making of simple graphs roughly correlating numbers by height with numbers by diameter. These are of limited applicability but in certain cases made enumerations usable.

Most conversions from one limit to another were done by constructing a stand curve or cumulative stand curve for the particular forest. The latter type was made from a table in which the total number of trees in an area was stated for successively larger limits, as 3 inches diameter and larger, 6 inches and larger, 9″+, 12″+, to whatever largest limit is appropriate. Each such total makes one point on the cumulative stand curve. The most useful of these curves was

one modified from a normal stand curve for old-growth deciduous forest made by the author and Audrey H. Benedict (see Benedict, 1945). From it could be found a "likely proportion" for converting from one limit to another. It seems to apply much more generally than to merely its own type of forest. Thus if an acre contains 92 trees of 8-inch diameter and larger, how many trees 3″ and larger are likely? On the graph, one reads 77.2 trees at 8″ and 151.74 at 3″. The likely number sought is $151.74 / 77.2 \times 92, = 181$.

If it was feasible to convert by each of several methods, this was done, and the results checked one against the other.

CHANGE OF SPECIES-NUMBER FOR CHANGED NUMBER OF INDIVIDUALS

Each conversion in number of trees involves a change in number of species, making a more difficult problem to solve. Two principal approaches may be used. The cumulative table from source materials lists not only trees at each of several diameter limits, but also numbers of species at the same limit. A graphic extrapolation or interpolation is usually satisfactory. This can be checked by another means. Graphs were arbitrarily constructed on semilogarithmic paper, plotting number of species against logarithm of number of individuals, in a family of concave curves patterned after those for Fisher's series in the publications by Fisher, Corbet, and Williams (1943), and Williams (1944). The arbitrary construction similarly spaces the curves evenly between an upper limiting logarithmic curve in which each individual represents a different species (maximum richness of composition), and a lower horizontal limit representing a single species for all possible individuals. In using such graphs a known combination of tree-number and species-number locates a point on or near a particular one of the set of curves. Following this curve right or left to the converted tree-number brings one up or down to the level representing its approximate number of species. Such an approximation is safer when the curve is followed left and down, and when the distance followed is small.

ANALYSIS OF PLOT-MAPS, AND RANDOM SPOTTING

If a description of vegetation includes a map of a large plot or more sizable area, showing individual plants identified by species, it is a simple process to subdivide it to derive figures for smaller plot-sizes. In this process, transparent or translucent overlays marked off into rectangles of appropriate area are convenient, permitting one to utilize the whole area for almost any plot-size chosen. It is sometimes feasible to use a rectangle with length equal to 1.414 times the width. Half-plots and quarter-plots thus have the same proportions as whole plots. Whatever the size, all units have the same shape, thus eliminating any possible fluctuations from this factor. It has been found that there is no significant difference due to shape of plot if length is no greater than twice the width.

If descriptions do not include maps, but give numbers of individuals for the different species in a stated area, a plot-map can be simulated by random spotting. It is a less laborious process if number of species is small. The one-to-several very abundant species can be omitted from all plot sizes which are certain to include one or more individuals of each. From analysis of considerable areas of forest it has been found that the size large enough to contain an average of 3 individuals is likely, in a simple community of few species, to include the species in 97 to 100% of the plots. In a moderately-mixed community with 20 to 35 species, the two or three more abundant species are likely to be less evenly distributed, and require a plot-size containing 6 individuals on the average, to give 97 to 100% frequency of occurrence.

The chance determination of a particular spot to represent the location of a plant was by means of a wide ring of heavy sheet brass. It was made to oscillate on the map, at the same time rotating slowly. When it came to rest, a mark on its outer edge determined the location of the plant.

In chance distributions of this kind, one is likely to be impressed by the fact that plants (of all species, or of any one more abundant species) are more evenly dispersed over the ground than would result from truly random location. Romell once remarked (1930: 592): "In almost any closed forest association, . . . there seems to be a tendency, easily explained by competition, for the trees composing the main stand to be equally spaced." Thus one finds it necessary, after locating about two-thirds of the required number of spots for the most abundant species, to omit further additions where spots are already clustered rather thickly, and to supply a few spots in the larger blank spaces. (The *exact* locations are in all cases the result of chance.) Thus an approach to the usual degree of evenness of distribution is attained. The opposite type of departure from random dispersal, due to aggregation, is much more frequently pointed out, but the common tendency for most species is toward fairly even spacing.

One application of this method, to forests of few species, was patterned on enumerations by E. A. Ziegler (1904) of blackjack oak (*Q. marilandica* Muench) and black oak (*Q. velutina*), in dunes of the Illinois River. For blackjack, Ziegler listed on 2 acres 295 oaks and 80 hickories (*Carya cordiformis*). Since 4 or 5 other species occur in this type, a hypothetical 16-acre sample was assumed to comprise 4 tree species, with 2858 trees 3 inches d.b.h. (diameter breast high) and over, of which only 10 belonged to the 2 uncommon species. From maps made by random spotting, then subdivided, species-numbers were found for 8 sizes of plots.

Ziegler's black-oak sample covered only 1 acre, with 93 trees in 4 species. Four other species are known to occur in the type, and possibly another 3. A map was made for an assumed 9 acres with 837 trees in 6 species. The species-area curve resulting from its analysis indicates a minimum area of 1144 milacres, only a little larger than Ziegler's sample. It has 4.34 species.

Ramaley's account of *Sarcobatus–Chrysothamnus* bush in the San Luis

Valley of southern Colorado (1942: 264), described 8 plots, each 40 × 80 feet, in a large stand on a salt flat 4 miles southwest of Mosca. The numbers of bushes he gave were spotted into rectangles of given proportions. Plots of about 147 milacres and larger plots (up to 734 milacres and presumably much larger areas) all have the same number of species, 4. The curve was drawn on the assumption that these 4 species are the only bushes within the district which can endure this extreme habitat. Consequently, the curve flattens abruptly into a horizontal line at 4 species, reaching that level at a little over one-eighth acre. The same dominants in less extreme habitats were accompanied by other species, bringing the total to about 10 bush species as shown in Ramaley's Table 2 (p. 245). From lists he made for 1000 0.1-sq.-m. plots in 20 locations, a quite different species-area curve results. This is of the usual form, and gives a minimum area of 46 milacres, with 3.8 bush species. The species-number climbs to 6.5 at 10 acres—still not a highly mixed bush assemblage.

RELATION OF FISHER'S SERIES TO SPECIES-AREA PROBLEMS

The important contributions of Fisher, Corbet, and Williams (1943), and of Williams (1944), illuminating relationship between numbers of individuals and numbers of species, and applying even more generally to many types of "hollow-curve" phenomena, will undoubtedly be of great usefulness in species-area problems. These two papers were not known to the author until December, 1945. Arbitrary species-individuals curves like those of the Fisher's series were thereafter the chief means of finding a species-number after converting from one tree-size-limit to another, in the manner already described.

It seemed that the Fisher's series and its quantity α, the index of diversity, should also become a principal means of amplifying incomplete data, providing additional points for a species-area curve. There is as yet no assurance that this is a dependable method, since it involves the assumption that the concave part of a species-area curve is practically identical with some one curve of the Fisher's-series form. A test of this assumption will be shown shortly.

It is obvious that a species-area curve as a whole cannot be replaced by a curve of the Fisher's series, since in the latter the steeper upper part of the slope is indefinitely continued at about the logarithmic rate. From a concave lower part it gradually becomes almost straight. A species-area curve for vegetation is clearly affected by added circumstances tending to retard the rate of species-increment, and thereby making its upper section convex.

Another question (with no present answer) is whether the species-individuals relation can help to solve species-area problems in vegetation for which no enumeration of individuals is at hand. (In some grasslands and certain shrubberies it is impracticable to distinguish or even to define plant individuals of certain species. Williams (1944) has essayed to apply the Fisher's series (without access to counts of individual plants) to Gleason's data for ground-cover in deciduous forest and in open parts of aspen woodlands in Michigan (1922, 1925), and to Beumée's ground vegetation in Tectona forests in Java (1922), as briefly tabulated by Arrhenius (1923). S-curves for these same vegetation-units were made for the present article.

A test of degree of correspondence between species-area S-curves and species-individuals curves having constant values of α throughout (called α-curves for brevity) has been applied to particular stands. These are in forest and shrub vegetations. Each enumeration covers a wide range of observed plot-sizes having dependable counts of individuals and species. A uniform ratio for successive plot-sizes was chosen for this test: half of a logarithmic cycle, each area being 3.162 times the preceding one. See Table 1. For each such area (A), the following quantities were noted: number of species (S), as read from the species-area curve; number of individual trees (3″ d.b.h. or over),

or bushes, or shrubs (N); and the index of diversity (α), found from S and N on a large-scale graph based on the table by Williams (1943:53). The values of α are likely to be in error by amounts up to 0.1 unit. For the first forest S, N, and α are given at each area; for other communities only the value of α.

TABLE 1. Values of α at Different areas for Six Communities.*

Area, *milacres*, $= A$		3.16	10.0	31.6	100	316	1000	3162	10000	31623	100000
Brownfield											
Woods	N		1.25	3.96	12.5	39.6	125.3	396	1253	3960	12527
	S			2.47	5.17	9.09	13.37	17.46	21.20	24.49	27.10
	α			3.0?	3.37	3.65	*3.80*	3.77	3.65	3.54	3.23
Reavis											
Woods	α		5.15?	*5.25*	4.94	4.92	4.85	4.56	4.28	4.07	3.82
Chamise											
chaparral	α		1.86	1.73	2.18	2.27	*2.87*	*2.87*	2.78		
Chamise–sage	α		2.80	2.85	*3.83*	3.41	3.38	3.30?			
California bush	α	1.58	1.50	1.50	1.58	*1.63*	1.62	1.58	1.50		
Philippia heath	α	3.25	3.82	4.30	4.62	*4.86*	4.73	4.42			

*For Brownfield Woods at 316 230 milacres, N = 39 600, S = 29.14, and α = 3.08. Data for Reavis Woods in Morgan County, Indiana, are from Potzger & Friesner (1940). The chamise chaparral stand is in the San Rafael Hills in southern California; the chamise-sage chaparral is on basal slope of Mt. Lowe; the bush is on a nearby alluvial fan. The *Philippia* heath in Mauritius was described by Vaughan & Wiehe (1941).— Note that values of α are far from constant. There seems to be little regularity among the several communities as to the area at which α reaches its maximum (shown in table by italic figures).

This table was supplemented by construction and study of graphs on which species-area data for four of these same communities were converted to species-individuals curves, and superposed on α-curves. Two of these communities appear in Fig. 3. The following facts were noted: (1) The Reavis Woods curve nearly coincides with the curve $\alpha = 5$ as far as the flex point at about 100 trees or 316 mlc., above which it gradually drops below this α-curve, being 1 species below it at 520 trees, 2 species below at 1200, and 5 species below at 5800 trees. (2) Each of 3 other curves in its lower course is nowhere far from a certain α-curve, but where it departs from this curve, the divergence is *upward*. The convex part of the community curve attains a height of 1 to about 4 species above the α-curve. In its upper course the community-curve gradually becomes less steep, crosses the α-curve, and continues the decline below it. (3) The place at which the upward trend away from the α-curve begins, varies in different communities. It is well below the flex point of the Brownfield and Philippia heath curves (at 45 plants or 359 mlc. for Brownfield, 35 plants or 3.9 mlc. for the heath). The upward divergence for the California bush is at 450 plants or 69 mlc., about at the flex point. (4) The community curves also display individuality in additional less-obvious characteristics.

One may tentatively conclude that the use of species-individuals curves for populations or areas *in the range below the flex point* is seldom likely to

lead to serious error. The description of a 1-acre or half-hectare plot of tropical forest with stated S and N gives one point for a species-area curve. From α-curves (or the similar arbitrary species-individuals curves often used in their place), additional S and N combinations for new points are readily obtained.

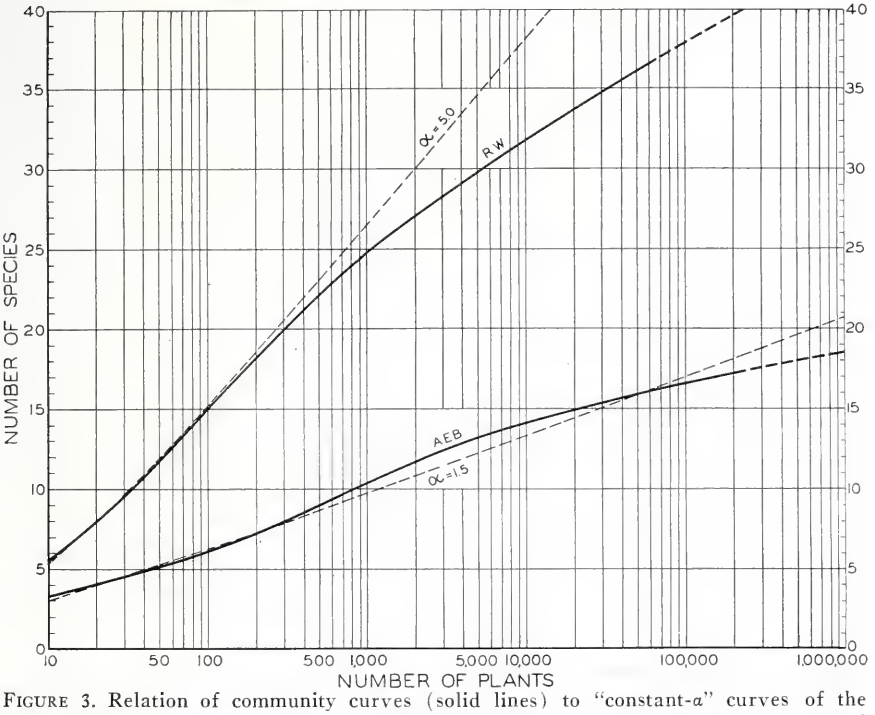

FIGURE 3. Relation of community curves (solid lines) to "constant-α" curves of the Fisher's series (broken lines). Both are species-individuals curves, the former adapted from species-area curves. The upper solid curve, for Reavis Woods, Indiana (data by Potzger *et al.*), is close to $\alpha = 5$ up to about 150 trees, and thereafter diverges downward from it. In another more common type, the community curve makes its first departure, in the upward direction, from the α-curve which its lower course roughly follows. Its convexity brings it to a crossing of the α-curve, as shown. The second community example is *Artemisia-Eriogonum* bush at the southwest base of San Gabriel Mountains.

If the description dealt instead with 25 hectares, so large an area would fall on the convex part of a species-area curve, well above the flex point. The conversion method just mentioned cannot be used in this case.

In spite of the considerable individualities of the community curves, and of the lack of agreement between such curves and α-curves in their upper sections, the author believes that Fisher's series, with its rational explanation of relation between numbers of species and numbers of individuals, is almost certainly the basis upon which additional characteristics of communities of rooted plants are superposed. Some of these characteristics are probably common to all estab-

lished vegetation; others constitute the qualities peculiar to certain types or to individual stands.

The suggestion is offered that certain types of field data, as those for Corbet's and Williams' collections of insects, or even line surveys in vegetation, and aggregates of well-separated very small plots, are less refractory statistical materials, so far as amenability to treatment by Fisher's series is concerned, than are the progressively larger one-piece areas of rooted vegetation here dealt with. The phenomena of competition and domination, with tendencies to nearly exclusive occupation by the relatively few most successful species; other factors contributing to difficulties and failures of free migration; the aggregation or "clumping" of individuals of one species; all these presumably operate differently in many plant communities as compared with those assemblages of animals which are less fixedly tied to particular areas.

It may prove that unsmoothed species-individuals curves for all sorts of organisms in all types of environments will reveal numerous peculiarities of individual populations which will lead to further investigation of the peculiarities. The curves should be based on direct field observations for that specific purpose, on populations of graduated sizes. Fisher's series should be a useful means of detecting and judging the peculiarities of curves and of populations.

A recent article by Preston (1948) considers the applicability of Fisher's series to collections of insects, records of occurrence of birds, etc. In his summary (p. 283): "Random samples of ecological or taxonomic assemblages indicate that the universes from which they are drawn have, at least approximately, the form of an ordinary Gaussian curve drawn upon a logarithmic base (a 'log-normal' curve). The sample has the same general form as the universe, but is decapitated."

RESULTS: REFERENCE AREAS AND THEIR SPECIES-NUMBERS

The areas and numbers of species as determined from about 240 species-area curves, are stated with extreme compactness in the tables which follow; but to give them meaning it is necessary to provide a background: character and location of the type of vegetation; by whom studied in the field, with citations of publications; habitat, leading species; partial statement of given data, of conversions employed, and of converted data serving as basis for the curve. Conversions, described in an earlier section, are shown by symbols:

C. Use of *curves,* species plotted against individuals, for a particular number of plants, or for a particular area.
E. To *effective* plot-size from nominal plot-size.
F. Use of *frequence* or constance data to find species-per-plot.
I. To *integral* equivalent area of compact proportions, from separated plots or from long strip.
L. Conversion of tree-diameter *limit,* to standard of three inches and larger.
R. Use of *random* spotting to approximate space-distribution of plants and species.

For some of the communities or stands studied there is no published statement; brief descriptions are provided.

Results were obtained for three reference areas: Ar, smallest representative area with its species-number Sr; Am, minimum area (= 5 Ar), with its species-number Sm (usually between 1.44 and 1.5 Sr); and Af, fair-sized stand (=50 Ar, or 10 Am), with its species-number Sf (=2 Sr). It is not necessary to give all six of these numbers. One area suffices, Am, expressed in both milacres and in square meters. (1 milacre or mlc. = 0.001 acre, or 43.56 sq. ft., or 0.2471046 sq. m.) Ar and Af, if needed, are found from the simple ratios given.

Readers will find Ar adequate for many purposes, since it almost always includes all the more abundant and generally distributed species of a stand. It is probably as large as the minimal area which has usually been adopted.

Since the ratio of Sm to Sr is not constant, both these species-numbers are given. Sf, if needed, is 2 Sr. For communities with known density of plant individuals (which may be restricted to one stratum, one growth-form, or to tree-sizes above a stated limit), the number of plants per acre is also given. The symbol for plants per thousand milacres is N1000. Number per acre is part of the background rather than a result, but aids in appraising reference areas and their species-numbers. Degree of dependability is also shown for each line of results. The number 1 indicates a solid basis of data, in many cases obtained for species-area purposes; a sufficient range of plot-sizes with directly-determined species-numbers. It is believed that two independent sets of observations so obtained within the same stand would agree within 10 or 12 per cent.

(See the two determinations for Trelease Woods in Table 2.) The number 2 suggests dependability intermediate between 1 and 3. The number 3 is used if the description gives only 1 or 2 areas or an aggregate of very small plots; if L-conversion is radical; if much dependence is placed upon C-conversions or upon assumption; or if the total sample is obviously inadequate. Some results with number 3 dependability may be less than 20% different from true values; on the other hand, they may range from half to twice the true value. Such results would be worthless if it were not for the fact that one of two apparently similar stands of the same type may have reference areas more than twice as large as in the other.

In setting forth results for particular stands or types, a table first summarizes results for each group of communities; the background follows the table. For forests, ground vegetation and tree-cover are considered in different groups. Data for trees are converted to a standard size-limit, 3″ +, (abbreviated form to designate all trees 3 inches d.b.h. or larger). Column headings signify: Am = minimum area; Sr = no. of spp. at Ar or smallest representative area; Sm = no. of spp. at minimum area; N1000 = no. of trees per acre (i.e., at 1000 milacres); D = degree of dependability.

TREES OF MID-LATITUDE FORESTS

TABLE 2. Old-Growth Mixed Deciduous Forests in Illinois and Indiana.

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Brownfield Woods, Ill.	4015	16 249	12.5	18.3	125	1
Trelease Woods, grid	3202	12 270	12.4	17.9	115	1
Trelease Woods, 12 plots	3337	13 504	12.4	18.2	126	1
S.e. of Palestine, Ill.	3019	12 218	13.8	20.3	160	2
Culled stand, Robinson, Ill.	2750	11 129	11.3	16.6	84	2
S.w. of Robinson	1302	5 269	17.8	11.5	155	2
Cox Woods, Indiana	2761	11 173	13.6	20.2	176	3
Reavis Woods, n. slope	1518	6 144	14.8	21.6	315	1
O'Hare Woods, n. slope	2563	10 372	13.9	20.6	172	1
Potzger's No. 37, s. slope	2680	10 846	15.8	23.2	223	1
Potzger's No. 39, s. slope	868	3 512	11.1	16.3	310	1
McCoy's R, Sullivan Co.	1968	7 962	15.8	23.2	231	2
McCoy's X, Greene Co.	1862	7 534	14.0	20.5	283	2
J, Jefferson Co.	2393	9 686	13.5	19.7	271	2
B, Jennings Co.	2697	10 915	10.1	14.8	138	2
Y, Daviess Co., bottomland	1542	6 239	18.3	12.3	241	2
S, Sullivan Co.	1674	6 774	7.2	10.6	183	2
W, Greene Co., flatwoods	1428	5 781	6.9	10.1	180	2
C, Jennings Co.	910	3 684	3.9	5.5	142	2
Q, s. Vigo Co.	2694	10 902	12.9	19.0	112	2

BROWNFIELD WOODS, N.E. OF URBANA, ILL. MESOPHYTIC PRAIRIE-BORDER TYPE. VESTAL AND HEERMANS (1945). 52-acre sample with 25 spp.; in 60-acre stand with notable surviving giant trees. *Acer saccharum* now most

abundant. *Quercus macrocarpa, Q. Muhlenbergii, Q. rubra* (northern red oak), 2 elms, 3 ash spp., *Tilia,* etc. 12 leading spp. No conversions.

Trelease Woods, 1 mile e. of Brownfield. Marberry, Mees, and Vestal (1936). Similar to Brownfield, but less well-drained. 27 spp. in 14.4-acre aggregate: 6.4-acre grid of 100-mlc. plots, + 10 well-separated oblong plots each 800 mlc. *Q. alba* is significantly absent from stands of this type. The second determination is from the 10 large plots plus 2 other 800-milacre plots within the grid of 64 100-mlc. plots.

Mixed mesic stand, on loess hills s.e. of Palestine, Crawford Co., Ill. S. R. Bradley (1932). At edge of Wabash River valley. 22 spp. in 10 100-mlc. plots; in ca. 36 acres. Conversions: F (6.9 spp. per plot), I (to 5 acres). *Acer saccharum, Liriodendron, Fagus, Q. rubra,* + 2 spp. (i.e., 6 leading spp.).

Culled stand, open and decadent, ca. 14 acres, at Robinson, Crawford Co. Bradley (1932). 4 leading spp., *Q. velutina, Prunus serotina, Q. alba, Q. imbricaria.* Neither mesic nor xeric. 15 spp. in 10 100-mlc. plots, 6 spp. outside plots. F (5.5 spp. per plot); I (to 4 acres).

Flatwoods, culled, s.w. of Robinson. Bradley (1932). Ca. 18 acres, with 16 spp. 3 leading spp., *Carya ovata, Q. imbricaria, Ulmus americana.* 14 spp. in 10 100-mlc. plots. F, I.

Cox Woods, Orange Co., s. Ind. Potzger, Friesner, and Keller (1942). Another notable remnant of virgin forest. 200 acres; ca. 60 acres in good condition, with ca. 28 or 29 spp. Leading trees *Acer, Fagus, Liriodendron, Juglans nigra, Q. alba, Fraxinus americana.* 18 spp. in 50 separated 100-sq.-m. plots (10-m. interval). Spp. per plot est. at 2.74. I-conversion (to 1581 mlc.).

Reavis Woods, and others in 5 miles of plots surveyed by Potzger and Friesner (1940). This survey in 5 counties south of the middle of Indiana consisted of alternate-plot strips of varying length and number in many stands. Plots are 10 × 10 meters (24.7 mlc.). Original field notes were generously made available for this species-area study. Data were thus found for various combinations of plots. Young trees of between 1-inch and 3-inch d.b.h. were omitted from the tabulations. The only conversion required was I, to integral equivalent area. — Reavis Woods is in Morgan Co. 389 trees of 22 spp. in 50 n.-slope plots. *Fagus, Q. alba, Acer, Carya* (3 spp.), *Q. rubra, Sassafras, Ostrya,* etc. Spp. per plot, 4.86. I, 50 plots to 1548 mlc. 3 intermediate plot-sizes. The basis for curves for the other stands was similarly estimated from these field data of Potzger and Friesner.

O'Hare Estate, 3 miles w. of Metamora, Franklin Co.; north-slope forest. Potzger & Friesner. 19 spp. in 50 plots. *Fagus, Acer, Liriodendron; Cornus florida* abundant.

Stand No. 37 of Potzger and Friesner. South-slope forest, 3 miles w. of Metamora. 24 spp. in 50 plots. *Fagus, Q. alba, Carya ovata, Acer, Fraxinus americana.*

No. 39 of Potzger and Friesner. South-slope forest, Franklin Co., 3.5 miles e. of Metamora. 17 spp. in 50 plots. Presumably calcareous site. *Q. Muhlenbergii, Q. rubra, Carya ovata, Fraxinus americana, F. quadrangulata.*

Scott McCoy's studies (1939) in mixed forests, mostly flatwoods. In s.e. Indiana (stands A to P, some in the district called "The Flats") and in s.w. Indiana (stands Q to Y). R, X, J, & B are well drained. Y is at times flooded; S, W, C, & Q are poorly drained. Most of these forests are on light-colored clayey soils. Each stand table summarizes 20 100-sq.-m plots, mostly in 2 alternate-plot strips. From McCoy's 25 forests, the 11 chosen for this study illustrate wide variation in many respects, especially in degree of richness of composition. Young trees between 1- and 3-inch d.b.h. were subtracted from the stand tables, thereby reducing somewhat the number of species from the listed total. Conversions: C, I (from 2000 sq. m. = 494.2 mlc., to 616.7 mlc.).

Stand R. Sullivan Co. 18 spp. in 20 plots. Most highly mixed of the 11. *Acer rubrum, Q. velutina, Q. rubra, Q. alba, Ulmus fulva, U. racemosa, Carya laciniosa, Fraxinus americana,* etc.

X. Greene Co. in sand-clay mixture. Pastured. 16 spp. in 20 plots. *Q. alba, Fraxinus americana, Carya ovata, Acer saccharum, Q. velutina, Ulmus Thomasii, Acer rubrum.*

J. Undisturbed. 14 or 15 spp. in 20 plots. *Q. alba, Carya glabra, Fagus, A. saccharum.*

B. Undisturbed. 10 or 11 spp. in 20 plots. *Fagus, Carya tomentosa, Liquidambar, Liriodendron, A. saccharum.*

Y. in black bottomland loam. 10 spp. in 20 plots. *Quercus palustris, Q. bicolor, Fraxinus profunda, Ulmus Thomasii?* (reported as cork elm, *U. racemosa*), *Acer rubrum.*

S. First of the 4 poorly-drained stands mentioned. 12 spp. in 20 plots. *Q. alba, Q. imbricaria, Q. palustris, Carya ovalis, C. ovata, Q. bicolor, Nyssa sylvatica.*

W. Stand with some disturbance from pasturing and cutting. 8 or 9 spp. in 20 plots. *Q. bicolor, Q. imbricaria, Q. palustris, C. ovata.*

C. Severely pastured flatwoods. Poorest in composition: 5 spp. in 20 plots. *Fagus, Liquidambar, C. ovata.*

Q. Stand with some cutting. 13 or 14 spp. in 20 plots: fairly rich, considering that this has lowest density among the 11 stands. *Q. velutina, Carya tomentosa, C. ovata.*

TABLE 3. Other Deciduous Forests in Illinois and Indiana.

Stand	Am. *mlc.*	Am. *sq. m.*	Sr	Sm	N1000	D
Black oak, Illinois River dunes	1 144	4 630	2.9	4.3	93	3
Blackjack oak, Illinois River dunes	1 800	7 284	2.0	3.0	179	3
Stony Lonesome, Bartholomew Co., Ind.	1 044	4 227	8.5	12.3	332	2
Ridge-top forest, Brown Co.	1 050	4 249	10.4	15.1	283	2
McCoy's I, cutover flatwoods	718	2 907	7.5	10.9	634	2
McCoy's V, young stand, Greene Co.	799	3 234	6.0	8.5	364	2

BLACK OAK DUNE FOREST, ZIEGLER (1904). This and the next illustrate simple composition in poor sites. In many places one or both oak species invaded sand prairie between 1830 and 1900. For a species-area curve, 6 species are assumed in 9 acres. Conversion: R, to give 8 plot-sizes. *Q. velutina* the only leading sp. A few *Q. rubra* (n. red oak). Other species rare. Low density.

BLACKJACK OAK DUNE FOREST, ZIEGLER (1904). Some fire-swept stands of this type are very scrubby, only 7-10 feet to tops of crowns. Ziegler's 2-acre sample with 2 spp. is assumed to be expanded to 16 acres with 4 spp. Conversion, R. *Q. marilandica* with ¼ to ⅓ as many *Carya cordiformis*.

XERIC MIXED STAND AT STONY (OR STONEY) LONESOME, BARTHOLOMEW CO., IND. AREA NO. 26 OF POTZGER AND FRIESNER (1940). Stony siliceous soil, south slope. 11 spp. in 20 100-sq.-m. plots. High density, trees mostly small. *Q. alba, Q. montana, Q. velutina, Fagus*. I, from 2000 sq. m. to 597 mlc.

RIDGE-TOP FOREST, 3 MILES E. OF NASHVILLE, BROWN CO. AREA NO. 7 OF POTZGER AND FRIESNER. They give 4 other small ridge-top samples, one (No. 45) with density of 425 trees per acre. In No. 7, 14 spp. in 22 plots in 1 alternate-plot strip. *Q. velutina, Q. alba, C. ovata, Fraxinus* sp., many small *A. saccharum*. Many species for the area, attributed to narrow site between two extensive forested slopes of different types. I, from 543 mlc. to 830 mlc.

MCCOY'S STAND I, JEFFERSON CO. 28-year stand replacing flatwoods cut in 1910. 10 or 11 spp. in 20 plots. *Liquidambar, Nyssa, Q. alba*. Highest density among the 11 stands. Representative for a young even-aged mixed forest.

MCCOY'S V, GREENE CO. Very young forest of fairly high density. A bottom-land type in black loam. 8 spp. in 20 plots. *Q. palustris, Acer saccharinum, Fraxinus profunda, Ulmus racemosa*.

NORTHERN PINE FORESTS

	Am. *mlc.*	Am. *sq. m.*	Sr	Sm	N1000	D
Pinus resinosa, Trout Lake, Wis.	678	2 743	6.3	9.2	372	2
Pinus strobus, near Wolf Lake, Wis.	860	3 480	5.8	8.4	255	1

NORWAY PINE FOREST ON THE POINT, TROUT LAKE, VILAS CO. N. WISCONSIN. J. E. POTZGER (1946). The computations and curves for this stand and the

next were made from Potzger's original field enumerations. The article in which his descriptions of these stands are included has since appeared (Potzger, 1946). Data for this stand, the Point Forest, are on pp. 213, 215, 220, 222, 235 (figs. 2 and 3). — Nearly undisturbed stand, ca. 40 acres. 9 or 10 spp. in 20 100-sq.-m. plots, *P. resinosa* dominant, in every plot, to 24″ d.b.h. *P. strobus* locally abundant, in 9 plots, 3-19″, mostly small. *Acer saccharum, A. rubrum, Q. rubra* (n. red oak), *Betula papyrifera;* 1 tree each of *Abies* and *Thuja.* Conversion: I, to 618 mlc.

White pine forest at Dairymen's Country Club, between Big Crooked and Wolf Lakes, Vilas Co., Wis. Potzger (1946). Data for this remarkable stand are on pp. 214, 220, 221, 224, 225, 236 (fig. 4).—Undisturbed stand, ca. 80 acres. 9 spp. in 50 plots, mostly in 2 strips. *P. strobus* dominant, in 46 plots; to 25″ d.b.h. *P. resinosa* in 35 plots, in places codominant, to 23″ d.b.h. *Acer saccharum, Abies balsamea, Acer rubrum;* 3 trees of *Tsuga.* Conversion: I, to 1736 mlc. — A later treatment of the ground layer, prepared from Table 23 in Potzger's article, appears in the section on stratified and mixed communities.

The fact that conifers grow to sizable trunk diameters with narrower crowns and smaller ground-space per tree than deciduous dicots, is reflected in the high density of these two stands (as compared with mature deciduous timber). This characteristic appreciably reduces the reference areas.

SCLEROPHYLL OAK WOODLAND, SOUTHERN CALIFORNIA

	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
60-yr. stand, Fern Canyon, 4900 ft.	319	1290	5.8	8.7	1 or 2

Evergreen oak woodland, San Gabriel Mts. U. S. Forest Service, 1935. Fern Canyon is tributary to San Dimas Canyon in the northeastern part of San Dimas Experimental Forest of California Forest and Range Experiment Station. Field notes and plot-maps were made in 1935 by R. W. Wiese & E. F. Wallihan, and were made available for this study at the Glendora Office of the Forest Service through the generosity of the Station and with the kind help of Mr. Jerome S. Horton. An earlier forest was destroyed by fire ca. 1875, and was succeeded by chaparral. This has been developing into forest again. The vegetation is a mixture of several growth-forms, shrubby oaks, large rounded oaks of small-tree stature, young trees of *Pseudotsuga macrocarpa* (only seedlings are in the plots), chaparral shrubs and bushes of several types. Two oak species are strongly dominant, *Q. Wislizeni* var. *frutescens* and *Q. chrysolepis.* They alternate rather than intermingle. The shrubs and bushes are very infrequent, only one, *Ceanothus integerrimus,* approaching 30% occurrence in plots.

Four species of next, though minor importance, are *Garrya Veatchii, Rhamnus californica* var. *ilicifolia, Penstemon ternatus,* and *Lonicera subspicata.* — The 99 plots, each 10 feet square, are in 3 groups separated by intervals of about 20 feet. Plots in each group are contiguous. They were established to study runoff

and erosion: the 9 down-slope strips are designated S.R.E. strips 341 to 349. Combinations of them provided 11 different plot-sizes. Since most of the oaks had several small stems, a 2-inch diameter limit was adopted. If a 2-inch stem *or* more than half of a crown occurred in the plot, that oak species was counted. The same convention, except that stem-diameter was disregarded, was applied to shrub and bush species. Recently-dead shrubs of *Ceanothus,* and seedlings of *Pseudotsuga,* were arbitrarily counted. Mean species-number per single 2.3-mlc. plot is 1.47. 8.0 spp. occur in 177 mlc.; 8.0 spp. again in all 99 plots (=227 mlc.) As might be expected, the reference areas are smaller than for forest, larger than for all but one of the chaparral and other shrub or bush vegetations studied.

SUBTROPICAL FORESTS

TABLE 4. Subtropical Forests, and Low-Latitude Mountain Forests.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Eugenia–Vaccinium, Bataan	280	1 133	12.9	19.3	747(?)	3
Mossy forest, Mt. Maquiling	764	3 090	12.1	18.1	332	2?
Mossy forest, G. Belumut, Johore	510	2 063	12.4	18.6	604(?)	3
Mixed subtrop. forest, Mauritius	1575	6 377	32.5	49.0	778(?)	2
Shorea–Plectronia, Bataan	1856	7 508	54.3	79.6	782	3
Quercus–Neolitsea, Mt. Maquiling	3441	13 920	44.5	65.2	257	3

EUGENIA–VACCINIUM FOREST, BATAAN PENINSULA, LUZON, 900-1265 M. ELEV. H. N. WHITFORD (1906: 652-666). 8 stations, 150 to 360 sq. m.; aggr. area 1792 sq. m., with 693 trees 3 m. high and taller (none reached 15 m.), in 65 spp. Sites differ. About 15 leading spp. (fewer in 1 plot): *E. congesta, E. acuminatissima, Acronychia laurifolia, Quercus* sp., *V. Cumingianum, Clethra lancifolia, V. Jagori,* etc. Plots individually spotted on species-area graph; curve drawn through swarm of points in same form as for less uncertain mossy forest on Mt. Maquiling. Conversion to 3″ limit suggests for same area (443 mlc.), 339 trees. A one-piece area of this size and of uniform site, probably has only 21 spp. Station A, largest (88.4 mlc.), most exposed, xeric, and steep, on volcanic peak with some fine soil, and at 900 m. elev., is closest to average condition represented by the curve. Station D is richest (Sm ca. 23); B is poorest (Sm ca. 17).

MOSSY FOREST, MT. MAQUILING, LUZON, 1020 M. ELEV. W. H. BROWN (1919: 98-109). 10 plots, each 5 × 10 m., presumably near one another. Size-limit, 1 m. height (but if it were 4 m., only 1 sp. fewer). 157 such trees of 17 spp. in 123.6 mlc. Brown also noted 21 spp. in 2500 sq. m. Only 3 spp. exceed 10 m., only 1 in 12-14 m. height-class. Abundant spp. (only 1 exceeding 8 m.) are *Astronia lagunensis, Clethra lancifolia, Cyathea caudata, Melastoma polyanthum, Itea maesaefolia.* L-conversion to trees of 5.25 m. ht. or 3″ d.b.h. and larger: 4.1 trees of 3.1 spp. in 12.36 mlc.; 61.5 trees of 12.6 spp. in 173 mlc. (1-piece area equiv. to 10 plots); 246 trees of 18 spp. in 741 mlc. Wide, distorted

crowns and loading of epiphytes are responsible for relatively low density. Perhaps this forest, like California oak woodland, can hardly be compared with ordinary "high forests."

Mossy forest, Gunong Belumut, Johore. Ca. 915 m. elev. near summit. R. E. Holttum (1924). Usable through density comparison with mossy forest on Mt. Maquiling for woody plants taller than 2 m. One 400-sq.-ft. plot and enumeration of larger trees. Ca. 9 leading spp., incl. 4 *Eugenias, Calophyllum canum, Podocarpus neriifolius.* Conversions suggest 4 spp. at 9.18 mlc., and 13.4 spp. at 129 mlc. Curve and results uncertain. A less extreme type than the preceding.

Mixed subtropical forest, Mauritius. 550 m. elev., above Black River gorges. Vaughan & Wiehe (1941). 1710 trees of 52 spp. (10-cm. diam. limit), in 10 separated plots, each 50 × 20 m., within one 800-ha. stand. Ca. 15 leading spp.: *Eugenia glomerata,* "Bois Caf-caf" (*Euphorbiaceae*), *Mimusops maxima, Aphloia theiformis, Elaeodendron orientale, Nuxia verticillata,* etc. Conversions: L, C. Est. spp. per plot, 31; 53 spp. in 2471 mlc. Notably high density. Type "probably akin to Tropical Lower-Montane Evergreen Rainforest of Burtt Davy."

Shorea–Plectronia Forest, Bataan. 450-900 m. elev. Whitford (1906: 642-645). 7 stations, 252 to 1440 sq. m., aggr. area 887 mlc. Sites differ. At greater elev. trees are smaller and density higher. 1011 trees 4 m. + (4 m. tall and taller) in 91 spp. Perhaps 13 leading spp. *Shorea polysperma* and other dipterocarps form 16% of stand. *Plectronia viridis* is the abundant sp.; dominates shady 2d story. Other notable spp.: *Memecylon edule, Calophyllum Whitfordii, Hopea acuminata, Thea montana, Eugenia* spp., *Cinnamomum mercadoi, Agathis philippinensis.* Stations are individually spotted on graph. Conversions, L: ratio is 192 trees 4 m. + to 132 trees 3″ +; C; I, a 1-piece area 2.5 × the aggregate is assigned same no. of spp., 83.9. — These 7 stations are given in Whitford's Table 19. In Table 20 are 4 stations of a large-tree variant, with density 501 instead of 782. These 4, with Station B from Table 19, fall almost on the curve for Brown's *Quercus–Neolitsea* association.

Quercus–Neolitsea Forest, Mt. Maquiling. 700 m. elev. Brown (1919: 76-, 96). Plot is 0.25 ha., with 577 trees and 71 spp. 1 m. ht. +; or 138 trees and 38 spp. 10 cm. diam. +. This is also "midmountain forest, moist-tropical, evergreen, 2-story." Perhaps, like the preceding two, it is transitional between tropical and subtropical. Leading top-story spp. include *Quercus soleriana, Cratoxylon celebicum, Neonauclea calycina, Weinmannia luzoniensis,* and *Ficus* spp. Second-story trees include *Oreocnide trinervis, Neolitsea villosa,* and *Saurauia luzoniensis.* Tree-ferns, rattans, and *Freycinetias* are prominent. Conversions, L and C: to 159 trees and 40 spp. 3″ +, at 618 mlc. Trend of curve judged from curve for preceding type.

TROPICAL FORESTS: PHILIPPINES, MALAYSIA

TABLE 5. Tropical Forests: Philippines, Borneo, Singapore, Ceylon.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Dipterocarpus–Shorea, Bataan	4 700	19 020	61.3	91.2	213.6	3
Dipterocarp forest, Mt. Maquiling	5 288	21 400	60.5	90.7	207.2	3
Anisoptera–Strombosia, Bataan	5 639	22 822	65.5	99.5	109.3	2
Lower Forest, Mt. Maquiling	6 560	26 547	58.5	86.4	183.2	3
Culled Dipterocarp, Mt. Maquiling	4 290	17 361	54.3	80.1	137.3	3
"Over-cut" forest, Mt. Maquiling	6 900	27 923	50.6	75.1	151.4	3
Dense parang, Lamao, Bataan	2 943	11 910	55.5	82.2	684.4	3
Grassy parang, Mindoro	21 400	86 603	26.3	38.8	54.6	3
Mixed rain-forest, Mt. Dulit	10 793	43 677	95.6	143.3	140.0	3
Marudi heath-forest, Sarawak	6 265	25 354	52.3	76.8	187.3	3
Koyan heath-forest, Sarawak	6 545	26 487	51.4	75.3	176.1	3
Southeast Borneo: Tanah Boemboe	6 550	26 507	61.3	91.6	130.7	3
Southeast Borneo: Pleihari	7 835	31 707	41.7	62.6	110.1	3
Secondary forest, Singapore	1 320	5 343	33.2	49.3	471.5	1
Sinharaja Forest, S.w. Ceylon	7 125	28 834	39.0	57.0	244.0	3

DIPTEROCARPUS–SHOREA FOREST, BATAAN. 340-410 M. WHITFORD (1906: 637-). Main plot on ridge at 340 m.: data by T. E. BORDEN. 1160 trees 4 m. + (ht.), 85 spp., in 8325 sq. m. 4 smaller plots at 410 m., 1 at upper limit for type. Top-story spp. are *Dipterocarpus grandiflorus, Shorea polysperma* and *S. contorta, Santiria nitida, Calophyllum Wallichianum,* and *Eugenia glaucicalyx.* L, C: 757 trees 3″ +, 77 spp. on 2057 mlc.

DIPTEROCARP FOREST, MT. MAQUILING. 450 M. BROWN (1919: TABLES 2-10). BROWN & MATHEWS (1914: TABLE 12). Main plot .25 ha., with 107 trees 10 cm. +, 43 spp. 22 top-story spp., incl. 3 dipterocarps: *Parashorea plicata, Shorea guiso, Hopea acuminata.* Also notable: *Celtis philippinensis, Canarium* (4 spp.), *Eugenia* (4 spp.); in 2d story: *Diplodiscus paniculatus, Dillenia philippinensis, Ficus* (4 spp.). 7 spp. in 3d story: 4 spp. over 2 m. high in 4th story as part of undergrowth. L, C: 128 trees 3″ +, 49 spp., in 618 mlc.

ANISOPTERA–STROMBOSIA FOREST, BATAAN. 80-250 M. WHITFORD (1906: 403-). Main plot 170 × 60 m. on diversified slope has 896 trees 4 m. +, in 120 spp. Plot on terrace of Lamao River, ca. 8000 sq. m., has 328 trees 4 m. +, in 92 spp. 6 other plots, 600 to 1500 sq. m. This richest forest of the Lamao Reserve occupies the zone above the lowest (the basal forest is *Bambusia–Parkia*). 31 top-story spp., incl. *Shorea* (3 spp. listed in preceding types), *Dipterocarpus vernicifluus, Anisoptera Vidaliana, Euphoria cinerea, Mangifera altissima.* In lower stories: *Strombosia philippinensis, Gnetum gnemon, Diospyros pilosanthera.* L, C (terrace plot): 216 trees 3″ +, 79 spp., in 1977 mlc.

LOWER FOREST, MT. MAQUILING. BELOW 300 M. ELEV. BROWN & MATHEWS (1914: 446-). On 1 ha., 403 trees 10 cm. +, ca. 63? spp. ("miscellaneous spp." not segregated). This type should be at least as rich in spp. as the main diptero-

carp forest just above. Ca. 9 leading spp.: *Diplodiscus paniculatus, Parashorea plicata, Diospyros* sp., etc. L, C: 453 trees 3″ +, 70? spp., 2471 mlc.

Culled dipterocarp stand, Mt. Maquiling. 200 m. elev. Brown (1919: 61-75). Plot .25 ha.: 887 trees 1 m. high and above in 129 spp.; 75 trees 10 cm. +, 42 spp. Of these 42, 10 are top-story spp., 28 are 2d-story, and 4 are 3d-story. L, C: to 93 trees 3″ +, 48 spp.

"Over-cut" forest, Mt. Maquiling, 140 m. elev. Brown & Mathews (1914: 444). Top story had been cut away. On 1 ha., 319 trees 10 cm. + diam., ca. 55? spp. (misc. spp. not segregated). *Diplodiscus* the only abundant spp.; *Garcinia binucao, Planchonia spectabilis, Dracontomelum Cumingianum,* etc. L, C: to 374 trees 3″ +, 60? spp.

Dense parang, Lamao, Bataan. 35 to 70 m. elev. Whitford (1906: 391). Parangs are secondary forest, following cutting. They differ greatly in composition and otherwise, depending on history and surroundings. 3 small plots, 2 to 3.5 km. inland, in lowland or *Bambusia–Parkia* formation. In 480 sq. m., 131 trees 4 m. +; 29 spp. 12 to 19 spp. in any 1 plot. Tall trees include *Aphananthe philippinensis, Anisoptera, Buchanania florida, Macaranga bicolor, Parkia Roxburghii.* L, C: for av. plot, 12 spp. in 39 mlc. Trend of curve is close to that of culled dipterocarp stand. Density is about 3 times that of old-growth forest.

Grassy parang, near Maujao, Mindoro, P. I. M. L. Merritt (1908: 39). Many parangs in Mindoro are scattered-trees-in-grass. This stand, with trees more closely spaced than is usual, is ¼ to ⅓ stocked. 1.73 ha., with 203 trees 10 cm. +, in ca. 25? spp. 7 or 8 leading spp., incl. *Sarcocephalus cordatus, Lagerstroemia speciosa, Barringtonia* sp., *Mitragyne diversifolia.* Other, chiefly parang spp.: *Albizzia procera, Antidesma* spp., *Grewia tiliaefolia, Bombycidendron Vidalianum.* L, C: on 4.27 acres, 233 trees 3″ +, 26.3? spp. Estimate for 1 acre: 55 trees, 15.5 spp. Reference areas prove to be extremely large. This illustrates the common and rather obvious influence of density: if trees are farther apart, larger area is required. Note contrast in size of Am as between this and the dense parang.

Mixed rain-forest, Mt. Dulit, Sarawak. 100-200 m. elev. P. W. Richards (1936: 21, 359). Main plot near Kapah River, 400 ft. square (1.418 ha., = 3672 mlc.), on steep side of ridge. 261 trees 8″ +, 98 spp. 2 profile strips, each 200 × 25 ft., on ridge-top and side-slope. Perhaps 16 leading spp. (listed under native names) incl. a sp. of *Shorea?* and one of *Dialium?*. Conversions: L & C: 513 trees 3″ +, in 112? spp., on 3672 mlc. Moderate density; rather large reference areas.

Heath forest, Marudi plot, Sarawak. A few meters above sea-level. Richards (1936: 28, 359). At edge of sandy plateau. 350 trees 8″ +, of 56

spp., on 3672 mlc. Of 7 abundant spp., 3 are dipterocarps. Others are *Agathis borneensis* and *Ternstroemia aneura*. L & C: 688 trees 3″ +, 69? spp. Somewhat higher density and less rich composition than in mixed forest of the same district are characteristics of heath forests (also known as "white-sand forests," "Wallaba forests," or moist-climate "caatingas"). These occupy similar sites in many tropical regions. Soil is sterile and leached; usually on well-drained uplands. In some of these forests, one species is most numerous or is dominant. *Agathis* forms notable stands in the Marudi district.

Heath forest, Koyan plot, Sarawak. Ca. 750 m. elev. Richards (1936: 28, 359). Deep, narrow, moist valley, of upper Koyan River, 329 trees 8″ +, in 55 spp., on 3672 mlc. Ca. 8 important spp., incl. *Agathis;* a relative of *Melanorrhoea; Casuarina sumatrana;* an oak or near relative; *Calophyllum?* (2 spp.); a dipterocarp. L & C: 647 trees 3″ +, in 67? spp.

Southeast Borneo: Tanah Boemboe. Van der Laan (1926, 1927), (as reported by Mildbraed (1930a: 55-56). Original not seen. Mildbraed's brief summary gives number of large-diameter trees, and number of species they represent, in each of 7 sample plots (presumably 1 hectare). They are in 4 localities. For the first (Tanah Boemboe), figures are given for mean, maximum, and minimum degrees of richness of composition. Diam. limit is 30 cm. for *Eusideroxylon Zwageri* and several important dipterocarps, and 40 cm. for other spp. For Tanah Boemboe (max.), "mean diam. limit" is est. to be 31 cm. (12.24″). For Pleihari (max.), est. is 32 cm. (12.63″). Only these 2 enumerations were considered amenable to conversion to 3″ diam. limit.

For Tanah Boemboe (max.), 91 trees 31 cm. +, in 47 spp. occupy 1 ha. Conversions, L and C: to 130.7 trees 3″ +, in 55.1 spp., on 1000 mlc. On 300 mlc., 28.5 spp.; on 100 mlc., 11.6 spp. Actual density of trees, 3″ +, may be somewhat higher, without change in no. of spp.

Pleihari. Van der Laan, in Mildbraed (1930a: 55-56). Max. and mean data are given. For Pleihari (max.), 73 trees 32 cm. +, in 29 spp., on 1 ha.; to 110.1 trees 3″ +, in 34.8 spp., on 1000 mlc. On 300 mlc., 18.7 spp., on 100 mlc., 8.6 spp.

Secondary forest, Singapore. I. H. Burkill (1919). Part of the Botanical Garden, on n. w. slope. Original forest was mostly cleared in 1869; weed trees grew up after ca. 1888, and were 30 years old in 1918 when 2 acres were cleared, and about ⅓ acre tabulated. 943 trees 3″ + in 2 acres; ca. 148 trees 3″ + of ca. 37 spp. in 314 mlc. (2 plots). 6 or 7 leading spp: *Arthrophyllum diversifolium, Rhodamnia trinervia, Symplocos fasciculata, Adinandra dumosa, Durio zibethinus, Elaeocarpus stipularis, Ficus polysyce.* Also *Cinnamomum iners, Artocarpus* spp. High density, small reference areas. I; to 157 trees in 333 mlc.

SINHARAJA FOREST, S. W. CEYLON. 579 M. ELEV. J. R. BAKER (1938). In largest remaining virgin tract of 90 sq. miles. Count of trees of girth 4 ft. or more at 4 ft. height, on half-acre squares. (Corresponds to size limit of 14.65″ d.b.h.) 25 trees in 13 spp. Spp. include *Durio zeylanicus, Myristica dactyloides, Calophyllum* (2 spp.), *Doona, Palaquium, Mesua, Mangifera zeylanica.* L & C: to ca. 122 trees 3″ +, in ca. 26 spp. Large reference areas; relatively poor in species composition.

TROPICAL FORESTS: WEST AFRICA

TABLE 6. Tropical Forests: West Africa.

Stand or type		Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Liberia: Evergreen Forest	Strip 1	9 478	38 334	51.2	77.6	91.4	2
	Strip 2	9 000	36 422	44.3	66.0	127.8	2
	Strip 3	10 430	42 209	47.6	69.2	122.4	2
Southern Nigeria:							
Mixed rain-forest	S. P. 1	12 345	49 959	30.4	45.0	189.1	2
	S. P. 2	10 730	43 423	39.4	59.4	244	1
	S. P. 3	9 195	37 211	53.4	79.2	181.7	1
Swamp forest	S. P. 4	10 715	43 362	34.0	50.0	167.3	1
Fernando Po: Mixed rain-forest		5 690	23 027	20.3	29.6	103.6	2
Kamerun: Jentsch; Primary forest							
Ngongnkeng	Plot VIII	5 592	22 628	108.8	162.2	251	2
Johann-Albrechts Höhe	II	6 065	24 544	89.0	132.6	202.4	2
Mundeck	V	6 142	24 856	78.7	117.2	242.9	2
Mujuka	VI	3 890	15 742	43.3	65.6	137.6	3
Bekili	III	5 115	20 700	61.0	91.4	217	2
Manoka	XII	11 550	46 741	24.4	36.9	136.5	3
Secondary forest (Kamerun)							
Njabi	XI	5 585	22 602	100	148.3	218.9	2
Johann-Albrechts Höhe	I	5 581	22 587	135.5	203.1	272.9	3
Bekili	IV	4 203	17 009	49.9	73.3	169.1	2
Likomba (Kamerun)	Plot VII	5 315	21 509	27.0	39.3	110?	3

LIBERIAN EVERGREEN FOREST, DUKWIA REGION. G. P. COOPER, 3D (1931). The study is based on 3 strips of half-acre plots. No. 1 has 16 plots, along southern side of a stand of "heavy bush," from which some trees have been cut. On 8 acres, 864 trees 2″ +, in 89? spp. Strip No. 2, 16 plots, extends north from an end of Strip 1. It is in heavy to medium bush, with a few openings. 1253 trees 2″ +, 74 spp. Strip No. 3 has 20 plots, and is in a different location. It includes some swampy spots with inferior growth. The largest trees are in No. 3. On 10 acres, 1448 trees 2″ +, 81 spp.—In the 3 strips, 9 or 10 large-tree spp. are notable, incl. *Anopyxis ealaensis, Berlinia* spp., *Canarium Schweinfurthii, Erythrophleum guineense, Lophira alata, Pentadesma butyracea.* About 19 small-tree spp. are abundant: spp. of *Carapa, Cola, Diospyros, Macrolobium, Polyalthia, Strombosia, Vitex, Xylopia,* etc. — Conversions: L & C, I. In strip 1, to 914 trees 3″ +, of 78 spp., in 10 acres. In strip 2, to 1278 trees 3″ +, of 67 spp., in 10 acres. In strip 3, to 1469 trees 3″ +, of 71 spp., in 12 acres.

Mixed rain-forest, southern Nigeria. P. W. Richards (1939). In each of 4 types, Richards listed trees 4″ + on a sample plot 400 ft. square, divided into 4 strips 100 ft. wide. He also tabulated 2 clear-felling strips, each 200 × 25 ft. (in plots 1 and 2). S. P. 1 is ca. 8 km. n. of Akilla, and is on nearly level upland, not far from Erioloma River. 606 trees 4″ + in 34? spp. About 8 leading spp. *Berlinia auriculata* and *Scottellia kamerunensis* have the most large and fair-sized trees. *Diospyros insculpta* and *D. confertiflora, Rinorea* sp., and *Picralima umbellata,* mostly smaller, are abundant. Conversions, L & C: to 695 trees 3″ +, of 35 spp., in 3672 mlc. For each of 3 smaller areas, species-numbers were proportioned from composite of values read from Richards' species-area curves for the other 3 types.

Richards' S. P. 2. Near Eluju village, ca. 5 km. n. of Akilla, on low tongue of nearly level dry land between 2 swamp areas. Plot is divided into 4 strips 100 ft. wide, the basis for Richards' species-area curve. 781 trees 4″ + in ca. 46 spp. Ca. 8 leading spp. *Erythrophleum micranthum* is no. 1 among large-tree spp. *Casearia bridelioides, Diospyros confertiflora,* and *Scottellia* also have some large trees. *Rinorea oblongifolia, Strombosia pustulata,* and *D. insculpta* are the abundant small trees.—L & C: to 896 trees 3″ +, 47.5 spp., in 3672 mlc. Species-numbers for 1, 2, and 3 100-foot strips were read from Richards' curve. As converted for trees 3″ +, they are 26.7, 37.3, and 42.3 spp.

Richards' S. P. 3. In Benin Province, within Okumu Forest Reserve. Ca. 50 km. w. of S. P. 1. The richest of Richards' mixed-forest plots. 582 trees 4″ +, in ca. 65 spp., in 3672 mlc. Not so many large and middle-sized trees as in S. P. 1. Spp. of *Strombosia* are most abundant, as are *Diospyros* (2 spp.), and *Pausinstalia brachythyrsa.* "Apako" (*Annonaceae*) has some large trees. Also notable are *Garcinia ovalifolia, Sapium ellipticum* and *Scottellia.* Ca. 11 leading spp. — L & C: to 667 trees 3″ +, ca. 67.3 spp., in 3672 mlc. *S* for 1, 2, and 3 strips (derived from Richards' curve): 33.2, 50, and 60.5 spp. — Mixed rain forests in both Liberia and S. Nigeria appear to be only moderately rich in species composition. Density is low to medium. Reference areas are comparatively large. Cooper considers the forests he studied to be "second-class evergreen forest."

Freshwater Swamp Forest, Ijebu Province. Richards' S. P. 4. Within Shasha Forest Reserve. Also 400 ft. square, in 4 strips. 536 trees 4″ +, in ca. 39 spp. Numerous large trees, especially of *Mitragyna stipulosa* and *Spondianthus* spp. Also notable: *Alstonia congensis, Casearia bridelioides,* and *Sarcocephalus nervosus.* No marked abundance for any of the small-tree spp. — L & C: to 614 trees 3″ +, in 40.3 spp., in 3672 mlc. *S* for 1, 2, and 3 strips (derived from Richards' curve), 23.5, 32.5, and 36.7 spp.

Mixed forest, Fernando Po. H. Burchardt, reported by J. Mildbraed (1933). Burchardt made a detailed survey of plants in 1 hectare on this island

which is close to the coasts of both S. Nigeria and Cameroon. Tree diam. was measured at 1-meter height. The description leaves doubt whether more than one or a few trees a little smaller than 10 cm. are present. One reads into a sentence by Mildbraed (on p. 949) that some smaller stems may not have been measured. The count gives 237 trees 10 cm. + in 23 spp. Of 9 or 10 large-tree species, *Pycnanthus kombo* and *Chrysophyllum africanum* are abundant. 3 species attain 130-cm. diam.; 7 spp. reach or exceed 80 cm. Of 13 or 14 middle-sized or small tree spp., *Strombosia grandifolia* and *Monodora myristica* are abundant. *Strombosia* thrives in deep shade. It has 105 of the 237 trees and is uniformly distributed over the plot.—Conversion (L & C) suggests a maximum of 256 trees 3″ +, in 25? spp., on 2471 mlc., — and 10.4 trees of 5.2 spp. on 100 mlc. — Mildbraed remarks on the low proportion of species to trees (Mischungsquotient) in comparison with Jentsch's Kamerun plots, and correlates it with strong domination by *Chrysophyllum, Pycnanthus,* and *Strombosia.* These species make up ¾ of the whole (by number): unusual in a tropical mixture. This factor and the rather low density increase size of reference areas.

Primary mixed rain-forest, Kamerun. Jentsch (1911). This much-cited study comprised surveys of half-hectare plots in 8 localities. (In 3 of these, and a 9th station, secondary forests were also enumerated.) Plots II, III, V, & VII were completely tabulated for all trees 7 cm. diam. and larger. Half of Plot VIII was thus tallied; for the other half, and for all of plots VI, X, and XII, the count included no trees smaller than 20 cm. The 7-20-cm. class was estimated for these areas from the complete tallies for other plots. Species-numbers are thus uncertain for some localities. Jentsch's account lists species for only one plot, V, using native names (for a few kinds, scientific names also).

Ngongnkeng: Plot VIII (p. 24). 1 km. s. of "Hauptlingsdorf Ngongnkeng auf lehnem bis steilen Nordhang." Elev. at the village is 590 m. Soil is laterite overlying gneiss. Tree-height is less than in most rain-forest. On the half-plot tallied, 75% of the stems are 7 to 20 cm. diam. Jentsch's est. for whole plot: 334 trees 7 cm. +, in 116 spp. on .5 ha. L & C: to 310 trees 3″ +, in 108 spp., on 1235.5 mlc. This type shows at the minimum area more species (162), than any other *primary* tropical forest among 31 studied. It is first also in no. of spp. on one acre: 104. A factor in this richness of Jentsch's Plot VIII is its somewhat unfavorable site, contributing to fairly high density. Its Mischungsquotient for trees 3″ + *at 1 acre* is 1:2.405 (1 sp. to 2.405 trees). In this measure of richness of composition, Plot VIII is surpassed by 3 secondary forests, by Whitford's *Anisoptera-Strombosia* (the richest: M. Q. = 1: 1.751) and by Cooper's Liberia Strip No. 1 (1:2.343).

Johann-Albrechts Höhe: Plot II (pp. 20-21). Ca. 2 km. n. e. of Johann-Albrechts Höhe station, on a s.e. slope. Lateritic loam over Schiefergestein (slate or schist). The 7-20-cm. size-class numbers only 51.5% of the stand. 260 trees 7 cm. +, in 91 spp.—L & C: to 250 trees 3″ +, in 88 spp. on 1235.5 mlc.

MUNDECK: PLOT V (PP. 21-23). In large expanse of nearly untouched forest near Mundeck station (km. 73 on north line of railroad). Level to east-sloping, "auf milden Lateritboden." 323 trees 7 cm. +, in 81 spp. This is the plot with detailed listing. 4 spp. are abundant, with 37, 33, 27, and 17 trees. 3 spp. (one is *Uapaca Staudtii*) have 9 trees each. 3 spp. (one is *Alstonia congensis*) have 8 trees each. — L & C: to 300 trees 3″ +, in 75 spp., on 1235.5 mlc.

MUJUKA: PLOT VI (PP. 21-23). In another large tract of Urwald s. of Hauptlingsdorf Mujuka, near km. 59. On level, porous, lateritic soil. Structure of virgin forest, with fewer small trees and high proportion of very large trees. One Njabibaum (*Mimusops djave*) was 207 cm. in diam., 68 m. high, volume 137 cu. m. Jentsch points out that for forest with so many large trees, a half-hectare plot is too small. 182 trees 7 cm. +, in 52 spp. — L & C: to 170 trees 3″ +, in 49 spp. on 1235.5 mlc. Comparatively low density.

BEKILI: PLOT III (P. 21). Within the cultivated district of the Mukonje plantation, in an area cut by ravines and always forest-covered. A several-storied primary stand. 293 trees 7 cm. +, 67 spp. L & C: to 268 trees 3″ +, 62 spp., on 1235.5 mlc.

SONG-BO: PLOT X, AND EDEA: PLOT VII (PP. 23-25). Tallies for these plots are so nearly the same as for Plot III that separate curves for them were not drawn. No. X is 2 days journey s. w. of Ngongnkeng near Song-bo village, 1 km. e. at ca. 250 m. elev. Level ground with Urwald. Laterite developed from gneiss. The plot included 7 trunks of Bokokólo, abundant nearby, some of giant size, with enormous knobby stems up to 5 m. diam. 292 trees 7 cm. +, 67 spp.; to 273 trees 3″ +, 65 spp. Likely value for Am: 5100 mlc., with 92 spp. Trees per acre, 221 (3″ +).

Plot VII is in the untouched primary forest n. of Edea. Level to gently east-sloping; stony to gravelly lateritic loam. No giant trees present. Under the largest trees *Lophira alata* is dominant. 8 or more other spp. are notable. 280 trees 7 cm. +, 66 spp.; to 264 trees 3″ +, 63 spp. Likely value for Am: 5140 mlc, with 90 spp. Trees per acre, 214.

MANOKA: PLOT XII (P. 27). On the densely forested Manoka peninsula. Level ground, sand with humus. Old-growth forest, from which some middle-sized trees have been cut. The large dominant trees of *Lophira alata* remain [1909]. Notably poor in spp. 184 trees 7 cm. +, 19 spp., in slightly larger plot, .51 ha. — L & C: to 172 trees 3″ +, 18 spp., in 1260 mlc. Lowest density among Jentsch's plots.

SECONDARY FORESTS, KAMERUN. JENTSCH (1911). Four of Jentsch's plots are in cut-over stands. One of them, No. IX at Ngongnkeng (pp. 16, 24-25), was not used for a species-area curve, since its canopy is an even-aged pure stand of Schirmbaum, *Musanga Smithii,* an opportunist species of openings and

clearings. If data were available for the understory (a mixture of many species), or for the canopy that may have developed since Jentsch's observations in 1909, the usual type of S-curve might be expected. Plots I and IV were in the same districts as Jentsch's old-growth Plots II and III.

NJABI: PLOT XI (P. 26). On left bank of lower Sanaga River, ca. 4 km. s. w. of Njabi village, in a long-settled district which is a mosaic of cultivated areas and of young, middle-aged, and old forests, mostly secondary. The plot is at ca. 50 m. elev., is level, in laterite with clayey subsoil. The stand is mostly of small trees, with oil-palms, weedy herbs, and many climbers. It is representative of an area 15 × 100 km. Njabi trees, *Mimusops djave,* are frequent to abundant over this area. 369 trees 7 cm. +, 147 spp., on .5 ha.— L & C: to 337 trees 3″ +, 135 spp., on 1235.5 mlc. Fairly high density added to inherently profuse mixture of species gives this stand the greatest number of species at minimum area (Sm = 203) and at one acre (129) among all the forests studied. Jentsch's primary stand on Plot VIII is second to this one.

JOHANN-ALBRECHTS HÖHE: PLOT I (P. 18). Location 2 km. w. of Kumba village on road to Buea. Ca. 245 m. elev. Lateritic loam on yellowish subsoil; level surface. An earlier stand was long ago removed by the natives, except for a few giant trees. Most trees (89.5%) are in the 7-20-cm. class. Weedy climbers are abundant. Two-story mixture, with ca. 11 top-story trees per hectare. 323 trees 7 cm. +, 111 spp., on slightly larger plot, .54 ha. — L & C: to 292 trees 3″ +, 104 spp., on 1334 mlc.

BEKILI: PLOT IV (P. 18). Near the Mukonje Plantation at ca. 150 m. elev., in level area. This a younger stand than on Plot I. It includes oil-palms scattered and in groups, weedy tall herbs, and climbers. 227 trees 7 cm. +, 60 spp., on .5 ha. — L & C: to 209 trees 3″ +, 58 spp., on 1235.5 mlc.

LIKOMBA FOREST, NEAR KAMERUN MOUNTAINS. CA. 50 M. ELEV. J. MILDBRAED (1930A, 1930B). An extensive tract, 14 × 3 km., flat over wide stretches. Mildbraed enumerated trees 30 cm. d.b.h. and larger, in each of 15 1-hectare Probeflächen. From 30 cm. to 7.62 is too large an interval for safe extrapolation, therefore data have been used for only one plot, No. VII, for which maps of 2 parts, each .4 ha., are given (1930b: 955-956), with complete listing of trees and species. On 1 ha., 9 spp. exceed 60-cm. diam. 6 spp. lead: *Pterygota macrocarpa, Lophira procera, Terminalia superba, Hylodendron gabunense, Alstonia congensis, Homalium africanum,* with possibly 2 others. Given: 81? trees 30 cm. +, in 27? spp., on 1 ha.; and 35.5 trees 30 cm. +, in 16 spp., on .4 ha. Conversion, L & C: to 270? trees 3″ +, in 33.9? spp. on 2471 mlc.; and 104? trees 3″ +, in 26.3? spp., on 988 mlc. Mildbraed states that this forest is floristically poor in comparison with Jentsch's and with some others he had seen. At minimum area, Likomba Plot VII is somewhat richer than Jentsch's Manoka Plot (39.3 to 36.4 spp.). At one acre it is far richer than Manoka (26.4 to 16.7).

Of Mildbraed's 14 other plots, only one, Likomba XII, has as many trees (30 cm. +) as VII. In XII, also in V, the no. of spp. represented by trees of this size is slightly greater than in VII. In the whole 4200 ha. of the Likomba tract he suggests a minimum of 300 woody spp. (A possible maximum is 430.)

TROPICAL FORESTS: SOUTH AMERICA

Table 7. Tropical Forests: South America.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Moraballi Creek, British Guiana						
Greenheart forest	8 440	34 156	76.1	114.4	246.9	3
Mixed rain-forest	8 550	34 601	79.2	118.9	203.9	2
Wallaba forest	10 000	40 469	64.1	96.1	285.9	3
Morabukea forest	19 500	78 914	70.2	103.5	143.1	3
Mora forest	21 650	87 615	68.2	100.7	141.0	3
French Guiana: Tollinche	10 070	40 752	58.6	85.7	130.7	3+
Camp Godebert	11 724	47 446	78.8	115.5	165.0	3+
Oyapock	18 050	73 046	98.0	141.5	148.7	3+
Eastern Brazil: Pernambuco	3 045?	12 323?	29.6	43.8	200?	3+
Southeastern Brazil: Lagoa Santa	3 475?	14 063?	58.8	87.8	200?	3+

Tropical forest, Moraballi district, British Guiana. T. A. W. Davis and P. W. Richards (1933, 1934). Forests of 5 different sites. Main plots are 400 × 400 ft., with trees 4″ + given in tables; also trees <4″ and >15 ft. height in 2 strips each 25 × 400 ft.

Greenheart forest, S. P. 4 (Sample Plot 4, in Table 5, p. 150; p. 119). The type is confined to porous reddish-brown sand, chiefly on ridge-slopes. *Ocotea Rodioei* forms 43.4% of trees 16″ +. *Pentaclethra macroloba, Eschweilera Sagotiana,* and *Licania venosa* are also abundant. Ca. 91 other tall-tree spp. Since greenheart areas are narrow, the table is for 2 plots, together equaling 160,000 sq. ft. On these, 773 trees 4″ +, in 94 spp. On the 2 25-ft. strips, 325 trees 15 ft. high +. Conversions L, C, and I: to 907 trees 3″ +, in 97 spp., in square plot of 3672 mlc. Also, 113 trees 3″ +, in 40 spp., in square of 459 mlc.

Mixed rain-forest, S. P. 3 (pp. 142-146; also Tables 1 & 2). This type covers much of the lower hilly lands, usually in rather sticky yellow-brown loam. *Pentaclethra macroloba, Licania* (3 spp.), *Eschweilera* (4 spp.), and greenheart, are leading spp. Ca. 85 other tall-tree spp. 644 trees 4″ +, in 90 spp., on main plot. On clear-felling strips 200 × 25 ft., 102 and 106 trees 15 ft. ht. +, in 36 and 39 spp. On strip 400 × 25 ft., 57 trees 40 ft. ht. + in 25 spp. — L, C, & I: to 749 trees 3″ + in 101 spp. on 3672 mlc.; 26 and 27 trees 3″ + in 16 and 17 spp., on 2 squares each of 114.8 mlc.; 43 trees 3″ + in 19 spp., on square of 229.5 mlc.

Wallaba or white-sand forest. S. P. 5 (pp. 122-126, Table 6). This most distinctive type, dominated by *Eperua falcata,* occupies white sand of high

hill ridges. Density is fairly high, a consequence of inferior site; buttresses are almost completely absent; canopy is fairly open, with less constantly humid air. *Catostemma fragrans* and *Licania buxifolia* are subdominant. *Cassia pteridophylla, Eperua Jenmani,* and *E. grandiflora* are also abundant. 919 trees 4″ + in 70 spp., on main plot. 399 trees 15 ft. ht. + on the 2 strips each 25 × 400 ft. — L, C, & I: to 1050 trees 3″ + in 77 spp., on 3672 mlc. 131 trees 3″ + in 33 spp. on square of 459 mlc.

Morabukea forest S. P. 2 (pp. 113-116, Table 3). Dominant species is *Mora Gonggrijpii.* The forest is dense, with heavy shade, commonly on lower slopes of smaller hills, and occupies much of the total area. Soil is heavy red clay, probably lateritic, finer than that of mixed type. Subdominants are *Eschweilera Sagotiana, Catostemma commune, Pentaclethra macroloba, Ocotea Rodioei, Licania venosa.* 460 trees 4″ + in 70 spp., on main plot. 176 trees 15-ft. ht. + on the 2 25-ft. strips. — L, C, & I: to 526 trees 3″ + in 69 spp. on 3672 mlc.; 66 trees 3″ + in 25 spp., on square of 459 mlc.

Mora forest, S. P. 1 (pp. 106-113, Table 2). The dominant *Mora excelsa,* larger and with higher buttresses than morabukea, occupies lowest ground, in strips along river-banks and creeks. These are flooded for considerable periods. Soil is usually moist through dry season. The type occurs also in shallow soil of some rocky slopes. Subdominant are *Pterocarpus officinalis* (corkwood), *Pentaclethra, Aldina insignis. Eperua Schomburgkiana* & *Macrolobium bifolium* are characteristic species. 462 trees 4″ + in 59 spp. on main plot; 154 trees 15 ft. ht. + on strips. — L, C, & I: to 518 trees 3″ + in 64 spp. on 3672 mlc.; 65 trees 3″ + in 23 spp. on square of 459 mlc.

Tropical forest, French Guiana. A. Bertin (1920). The valuable report by Bertin appeared at first to be unusable, since his 40-cm. diam. limit requires so radical an extrapolation in converting to 3-inch limit. Conversion was tried experimentally by three methods, using stand-graph and cumulative stand-graph made from Bertin's Table 3, and the cumulative graph for Brownfield Woods. The ratios found for number of trees 3″ + to number of trees 40 cm. (15.75″) + are: 3.26 or higher, 3.78 or higher, 5.64. These ratios give from Bertin's 2676 trees 40 cm. + on 34 hectares the following numbers of trees per acre: 103.8 or more, 120.3 or more, 179.6. If one adopts as a likely estimate of density, 165 trees per acre, the total for Bertin's 34 ha. becomes 13,860 trees 3″ +. The ratio of this number to his 2676 is 5.181. This multiplier makes possible a probably fair comparison of Bertin's forests with others. Its application to 3 of his districts follows.—These treatments of Bertin's forests and of two Brazilian examples should be regarded as speculations more than as computations. They are accordingly assigned in Table 7, a dependability rating of 3+ rather than 3. These forests are not used in summarizing data for tropical forests in general.

Tollinche and Crique Sparouine district, Maroni (pp. 16-17, Table 4). The species with the most very large trees is *Caryocar glabrum;* most

abundant are *Dicorynia paraensis,* Bois grage blanc, Simarouba, Goupi rouge franc (*Goupia* sp.), Grignon franc, and Maho cigare. The total is 934 trees 40 cm. + in 75 spp. on 15 ha. In Table 8 (pp. 29-32), a 1-ha. parcelle has 74 trees 40 cm. + in 27 spp. — Conversion for 15 ha., L (multiplier 5.181) & C: to 4841 trees 3″ + in 104.5 spp., on 37.07 acres. The 15 ha. is probably a composite.

District of Camp Godebert and Crique Accarouany, Maroni (pp. 13-15, Table 3). *Eperua falcata, Dicorynia, Ecclinusa sanguinolenta, Licania galibica,* and *Manilkara balata* are most numerous. The 34 ha. probably is a composite of separated areas representing several types. 2676 trees 40 cm. + in 118 spp., on 34 ha. A 1-ha. parcelle has 86 trees 40 cm. + in ca. 18 spp. Conversion for 34 ha., L & C: to 13,860 trees 3″ + in 152? spp., in 84 acres.

District of Oyapock (Crique Balaté and environs de St. Georges) (pp. 21-23, Table 6). *Goupia glabra, Dicorynia, Eperua, Manilkara, Licania,* and *Ecclinusa* are commonest. The 9-ha. sample, probably a composite, has 638 trees 40 cm. + in 98 spp. These convert to 3307 trees 3″ + in 147? spp., on 22.23 acres. There is also a 1-ha. parcelle with 58 trees 40 cm. + in 25 spp.

It is probable that the reference areas for Bertin's prospections are larger than would be the case if each represented a single forest type. For such a type the reference areas would perhaps be .5 to .7 of the size found for one of the three sets of data here treated.

No plot data for Amazonia are known to the writer. F. F. Netto (1945: 38) says: "In the entire Amazon Valley the flora is so intermixed that if a sq. km. of ground could be marked off only a single specimen of any one of the different kinds of trees probably might be found therein. Nevertheless, zones do exist where a single or sometimes a group of species occur in denser stands. For example, the oil palms are numerous in the region of the Islands; Brazil nut in the Middle and Upper Tocantins River; and "jarina" [ivory-palm] in the Middle Solimões. A further exception must be made for the "guaraná," which is found only in the municipality of Maués and vicinity, in the State of Amazonas. For the others dispersion is the rule . . . ."

Pernambuco forest, eastern Brazil. V. Sobrinho (1937). The original report was not accessible; in the abstract by B. E. Dahlgren one finds that the forest is old-growth, with all age-classes, and composed of both hard and soft timbers. Low vegetation in the area studied had been cleared out by fire. A burnt area of 5000 sq. m. was studied; 704 trees of unspecified diam.-limit represent 49 spp. Av. interval between trees is 7 m. (est.). The mixture must be thorough, since the 3 commonest trees, *Carapa* sp., *Heliotropium* sp., and *Protium* sp. occur in small numbers: 35, 31 and 27 (93 of the 704). Conversion to 3″ limit is impossible with no more information as to size of trees. The enumeration presumably includes saplings and arbuscules; with the more sizable

trees also, density as given is 569 per acre. If one assumes that on the basis used for other forests, this one is moderately dense, a likely number per acre (based on 3″ diam.-limit) is 200. On this assumption, C-conversion gives 34.7 spp. for 200 trees, 22.2 spp. for 60 trees, 12.1 spp. for 20 trees, on 1000, 300, and 100 mlc. From these figures a tentative species-area curve was made, and from it tentative reference areas computed.

Lagoa Santa, southeastern Brazil. E. Warming (1899). A much-cited but not very explicit statement of tropical *richesse florale*. Where Warming could study trees as they were being cut down, he found, in 6 different cases, that 50-250 trees represent 27-91 spp. It was thought interesting to treat this example in the manner of the preceding, using the same assumption of 200 trees 3″ + per acre. The median number of trees, 150, was found by C-conversion to represent 45.4-73 spp.; mean is 59.2. If the sizes included by Warming are the same as those listed by Sobrinho, 150 such trees occupy 263.7 mlc. The number of trees 3″ + which occupy this area is 52.74. C-conversion suggests 34.7 spp. for 52.74 trees. For 200, 50, and 20 trees, species-numbers are 66.7, 37.5, and 16.7, on 1000, 300, and 100 mlc. As thus computed, floristic richness is above average, but not exceptional.

SUBTROPICAL THICKET AND HEATH, MAURITIUS

	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Sideroxylon thicket	92.4	374	44.8	69.0	15 520	1
Philippia heath	163.9	663	18.4	28.0	8 920	1

Sideroxylon thicket, Mauritius. R. E. Vaughan & P. O. Wiehe (1941: 150). This thicket is an early stage of mixed forest, and is placed with shrub vegetation rather than forest because the size and spacing of plants, and sizes of reference areas, are closer to shrub types than to forest. Two dominant species, *S. Bojerianum* and *S. puberulum,* form open canopy 8-10 m. high. Under it is a dense closed stratum with ca. 80 spp., and 3500 individuals 50 cm. ht. + in 1000 sq. m. Beneath this are herbs and small shrubs. More abundant species are *Eugenia orbiculata, Securinega durissima, Erythrospermum mauritianum, Antirrhoea verticillata, Aphloia theiformis, Erythroxylon laurifolium.* Vaughan and Wiehe give species-area curves drawn to linear coordinates.

Philippia heath, Mauritius. Vaughan & Wiehe (1941: 148). The term heath is appropriate, since *Philippia* is in *Ericaceae.* This shrub formerly covered large areas. It is adapted to unweathered lava exposed to violent rains and to long periods of tropical sun. Three species peculiar to it are dominant: *Philippia abietina, Phylica mauritiana, Helichrysum yuccifolium. Aphloia theiformis* is next abundant after *Philippia.* The semi-open shrub stratum is 1-3 m. high. Under it are *Gleichenia, Lycopodium,* and *Cladonia.* The authors give species-area data for 9 plot-sizes, from 4 spp. in 4 sq. m. to 30 spp. in 1000 sq. m. The size-limit is presumably 1 cm. diam. or 50 cm. height.

CHAPARRAL AND BUSH, CALIFORNIA

For much of the data on chaparral, the writer is indebted to the California Forest and Range Experiment Station. By chaparral is meant the evergreen shrub of fairly high rainfall belts of California foothills and mountains, in which species of *Adenostoma, Ceanothus, Arctostaphylos,* or *Quercus* usually dominate. By *California bush* is meant a highly variable complex of bush communities. (Bushes have many small, short-lived, not-very-woody stems, in contrast with the fewer, thicker, woodier, and longer-lived stems of most true shrubs.) California bush is more inclusive than the several associations comprising the coastal sage-brush formation or climax of Clements. *Artemisia californica* and bush species of *Salvia, Eriogonum, Lupinus, Eriodictyon, Diplacus,* and *Aplopappus* are among the notable plants. Their leaves are commonly specialized in various ways, many being resinous, strongly aromatic, heavily tomentose, revolute, or linear. As compared with chaparral, bush commonly occurs in low-rainfall zones or in drier sites, in finer soil or on less steep and rocky slopes, or at lower elevations, or in more recently disturbed areas. In places it forms a narrow border or a broad zone between chaparral and grassland. At least some bush types and most forms of chaparral are well adapted to fire and prevail where fires are recurrent. Some species are members of both formations. The type designated by J. S. Horton as chamise-sage is intermediate.

In some chaparral and bush areas it is impracticable to distinguish and thus to tally plant individuals. The numbers per acre given in four instances in Table 8 are very rough estimates.

TABLE 8. Chaparral and Bush, California.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Mixed chaparral, Bell Canyon	88.6	359	13.5	19.7		3
Oak chaparral, Bell Canyon	79.0	320	13.5	19.7		3
Oak chaparral, Tanbark	262.1	1061	15.0	22.6		1
Chamise type, Bell Canyon	87.8	355	11.7	17.0		3
Chamise type, Tanbark	186.2	753	12.0	17.9		2
Chamise type, San Rafael Hills	450.0	1820	9.9	14.6	2570?	1
Chamise-sage, Bell Canyon	56.5	229	8.7	12.6		3
Chamise-sage, base of Mt. Lowe	273.8	1108	13.2	19.5	3860?	1
Mixed bush, Verdugo & S. R. Hills	136.1	551	9.3	13.8	4500?	2
Bush near Mt. Lowe	134.3	543	6.9	10.2	6520?	1

MIXED CHAPARRAL, BELL CANYON, SAN GABRIEL MOUNTAINS. J. S. HORTON (1941: 461-463). Bell Canyon is tributary to Big Dalton Canyon, which opens at the steep south front of the San Gabriel Mts. between Glendora and San Dimas. In four small watersheds (catchment areas) forming the amphitheater-like head of Bell Canyon, 222 1-milacre plots were established near horizontal trails at four levels, 2550 to 3300 feet, and spaced at 132 ft. intervals. These plots are in four chaparral types, only 20 representing the mixed type. 20 species

of woody plants, not all of the size and growth-form characteristic of chaparral dominants, are represented in the plots. Average number of species per plot, readily found from Horton's frequency tables on pp. 462-463, is 4.10. 40.2% of the ground surface is bare. *Ceanothus crassifolius, Photinia arbutifolia,* and *Arctostaphylos glandulosa* are dominant, making 50% of the plant cover. 9 other species contribute much to the bulk of the vegetation, among them *Adenostoma fasciculata* (chamise), *Salvia mellifera* (black sage, a bush), and *Garrya Veatchii.* I-conversion from aggregate area of 20 separated plots gives a one-piece equivalent area of about 96 milacres. Thus for this and 3 other types in Bell Canyon, 2 points for a species-area curve are available.

Horton has since studied this same type at higher elevations. He now designates it broad-leaved chaparral, principally because the needle-leaved chamise is absent or infrequent. *Q. dumosa* is also insignificant in broad-leaved chaparral; and in locations other than Bell Canyon *C. crassifolius* is unimportant.

A somewhat different chaparral mixture on a northeast slope at Stough Park at ca. 1500 ft. elev. in the middle part of the s. w. side of Verdugo Hills, observed in 1944, has 17 spp. in 1 acre. *Quercus dumosa* is abundant. In addition to some of the Bell Canyon spp., *Rhus integrifolia, R. laurina,* and the thicket-forming semi-woody grass *Elymus condensatus* are present.

Oak chaparral, Bell Canyon. Horton (1941: 461-463). 33 of the 222 plots are dominated by *Quercus dumosa, Ceanothus crassifolius,* and *C. oliganthus,* making over half of the cover. *Salvia, Cercocarpus betulaefolius, Photinia, Prunus ilicifolia,* and 3 other species are important. The oak shrubs are broader and taller than others. Oak chaparral and mixed chaparral are the least xeric types of the district. The average 1-milacre plot has 4.94 spp. Aggregate species-number is 22. One-piece equiv. area is 150 mlc.

Oak chaparral, Tanbark Erosion Plots. Data by Calif. F. & R. E. S. The location is near Tanbark Flat, elev. ca. 2750 ft., in north fork of San Dimas Canyon. Slope is to the east, ca. 33%. Soil is deep, with no exposed rock. It is a less xeric exposure than Bell Canyon. The plots are in down-slope strips, each 10×110 ft., in contiguous groups of 3, with 3 such groups close together (strips 321-329). Strip 321 is of a different type. Strips 323-329 form the present sample of oak chaparral. Original data were studied at the Glendora office, and average species-number per plot was determined for each of 22 sizes, from 2.44 spp. at 100 sq. ft. (2.295 mlc.) to 21.0 spp. at 172.8 mlc. The same 3 species dominate as in Bell Canyon. *Salvia* is absent, *Cercocarpus* is locally abundant, and *Penstemon cordifolius* is locally frequent. *Arctostaphylos glandulosa* is replaced by *A. glauca.* — Fig. 2 (p. 5) is the S-curve for this oak chaparral.

Chamise type, Bell Canyon. Horton (1941: 461-463). This is the extensive type, occupying 147 of the 222 plots. *Adenostoma* and *C. crassifolius*

dominate; *Salvia mellifera, Eriogonum fasciculatum,* and *Q. dumosa* are the 3 other leading species. 51.8% of the ground surface is bare. Spp. per 1-mlc. plot, 3.52. Aggregate species-number is 22. One-piece equiv. area is 500 mlc.

Chamise type, Tanbark Plots. Data by Calif. F. & R. E. S. One strip 10 × 110 ft., No. 321 of the 9 strips mentioned with oak chaparral. Between strips 321 and 323 is a change in direction of slope, giving more xeric exposure to No. 321. From original plot-maps and records at the Glendora office, species-numbers for 6 plot-sizes were found, from 2.91 at 2.295 mlc. to 10.0 at 22.95 mlc.

Chamise type, San Rafael Hills. A. G. Vestal, August, 1944. These and the Verdugo Hills form an outlier of the San Gabriel Range near its southwest base. They are separated from the range by an alluvium-filled pass 10 miles long, and 1 mile or more wide, trending northwest-southeast, in which lies a line of towns from Sunland to Flintridge. The smaller, more easterly San Rafael Hills are separated from the more massive Verdugo Hills by Verdugo Canyon. The area studied is at ca. 1200 ft. elev. near the southeast extremity of San Rafael Hills. It comprises 12 contiguous plots 20 ft. square, plus an adjacent area equal to 12 plots. Analysis provided species-numbers for 6 sizes, from 4.75 at 9.18 mlc. to 13.0 at 220.3 mlc. *Adenostoma* is dominant. *Salvia mellifera* and *Eriogonum fasciculatum* are abundant enough to bring this stand close to the chamise-sage type. *Cercocarpus* and *Yucca Whipplei* are moderately frequent.

Chamise-sage type, Bell Canyon, Horton (1941: 461-463). This xeric type occupies 22 of the 222 Bell Canyon plots. 76.1% of the surface is bare. *Eriogonum, Adenostoma,* and *S. mellifera* dominate. Other leading species are *C. crassifolius, Eriodictyon trichocalyx,* and *S. apiana.* Spp. per plot, 3.10. Spp. in 22 plots, 14. Equiv. one-piece area, 105 mlc.

Chamise-sage, base of Mt. Lowe. Vestal, August, 1944. Xeric slope at ca. 1800 ft. elev., southwest part of San Gabriel range at Altadena. The area had been burned a few years earlier. Dead stems were still evident. Dominant shrubs of *Adenostoma* were 2.5-5 ft. high. *S. apiana, Artemisia californica,* and *Eriogonum* are the principal bush species. 20 6-mlc. plots, + 2 18-mlc. plots were listed. 6-mlc. plots are 19.23 × 13.59 ft., a size convenient for shrub vegetation. Analysis gave species-numbers for 10 plot-sizes, from 6.0 spp. at 6 mlc. to 19 spp. at 240 mlc.

A chamise-sage area at 1500 ft. elev. on a northwest slope near the northwest end of San Rafael Hills close to Montrose, has 13 spp. in ca. 400 mlc. Another chamise-sage south slope at Stough Park at ca. 1500 ft. elev., in the Verdugo Hills, above Burbank, has 15 spp. in a 400 mlc. sample.

Mixed bush, Verdugo and San Rafael Hills. Vestal, August, 1944. The curve for moderately to highly mixed bush is a composite for four stations

within a few miles of one another. One is an area of disturbed bush near southeast end of San Rafael Hills, with 19 spp. in 3 acres. *Artemisia, Eriogonum, Lotus scoparius, Senecio Douglasii, Salvia mellifera* are notable. Also present are *Adenostoma* and a few other shrubs, probably survivors from former chaparral. — No. 2 is an alluvial flat sloping slightly southwest at base of northwest end of San Rafael Hills, just s. of Montrose. It is below hills with chamise-sage cover, and receives an infusion of shrub species therefrom. Parts of this flat are disturbed with thinned and weedy bush. It has 22 spp. in 6 acres. *Artemisia, Eriogonum, Salvia apiana, Aplopappus (Ericameria) Parishii, Rhamnus crocea* var. *ilicifolia, Senecio,* are the common species; *Tetradymia comosa* and *Lonicera subspicata* are conspicuous. — No. 3 is the flat, open, disturbed lower part of Sunset Canyon in Verdugo Hills above Burbank. It has 18 spp. in 2 or 3 acres. — No. 4, in many ways notable, is an alluvial flat between low mountain spurs at Stough Park, higher in a branch of Sunset Canyon. It is 100-200 ft. wide, 1800 ft. long. It is slightly trenched by recent erosion. Chaparral covers the adjoining spur ridges. The flat has rather rich bush cover, also with infusion of chaparral shrubs, making 25 spp. in 8.3 acres. Among species not in the other 3 stations are *Rhus integrifolia, R. trilobata, Diplacus longiflorus,* and *Aplopappus (Ericameria) pinifolius.* In moderately mixed bush, as the curve for this composite suggests, one may expect 13 spp. in 0.1 acre, 18 spp. in 1 acre, and 22.4 spp. in 10 acres.

Bush, near base of Mt. Lowe. Vestal, August, 1944. This bush occupies the head of an alluvial fan, below the steep basal slope of the San Gabriel Range, near Altadena. *Artemisia* and *Eriogonum* are the dominants. *S. apiana* is locally abundant. *Lotus scoparius* occurs in interspaces among the larger bushes. 20 3-mlc. plots, and 10 6-mlc. plots, all contiguous, with 3 larger areas (one including the plots), make up the sample. The 3 larger areas are each ca. 878 mlc. There are 14, 13, and 12 spp. in these 3 areas, only 15 in all. Species-numbers for 14 plot-sizes were obtained, beginning with 4.4 for 3 mlc. and 5.35 for 6 mlc. Reference areas are larger than might be expected. This is attributed to the nearly complete domination by two species, leaving little room for individuals of others.

MEDITERRANEAN SHRUB VEGETATION

Two sources of plot data for maquis and garigue have been used for curves, samples being very small in all of the 7 localities. The resulting reference areas are markedly smaller than those found for chaparral and bush in California. It can not yet be said that this difference is real.

Quercus pubescens–Spartium–Cistus. Monte Gauro, near Naples. 200 m. elev. J. Y. Bergen (1903). Bergen's Plot E is described as open thicket on an east slope. The oaks are dominant, and grow to 3.5 m. high. 32 of them occur on a plot 10×10 m. *Spartium junceum* (22 indivs.), *Crataegus* (11),

TABLE 9. Mediterranean Evergreen Shrub and Bush.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Quercus pubescens, Monte Gauro	27.67	111.9	5.53	7.13	5 704	3
Arbutus–Q. coccifera, n.e. Spain	6.64	26.9	7.52	11.07		3
Arbutus–Pistacia, etc., Capri	8.00	32.4	6.91	10.08	70 060	3
Erica multiflora, etc., s. France	6.65	26.9	10.77	15.76		3
Myrtus, etc., Pozzuoli, Solfatara Hill	6.50	26.3	5.61	8.18	59 060	3
Spartium–Cistus, etc. Capri, n.w. slope	10.00	40.5	5.34	7.74	29 610	3
Thymus, etc., near Lerida, n.e. Spain	6.70	27.1	4.91	7.10		3

Cistus salviaefolius (62), 3 other shrubs (14). 141 plants in 7 spp. on 24.71 mlc. For this and 3 other of Bergen's plots likely species-numbers for smaller areas were found from species-individuals curves (C-conversion). It is possible that Bergen counted each stem or shoot as a plant individual.

ARBUTUS–Q. COCCIFERA: MOUNTAIN MAQUIS AT TOP OF TIBIDABO NEAR BARCELONA, N. E. SPAIN. C. RAUNKIAER (1916: 235, TABLE 4). In order of frequency in 50 separated plots, each 0.1 sq. m. (est. effective plot-size 0.5 sq. m.) : *Arbutus unedo, Q. coccifera, C. salviaefolius, Erica arborea, Calycotome spinosa,* and 7 other spp. incl. *Pistacia, Q. ilex, Q. pubescens.* Spp. per plot, 3.24. One-piece equiv. area, 10.69 mlc., with 12 spp. Two points available for a curve for this and Raunkiaer's other localities.

ARBUTUS–PISTACIA–QUERCUS–ERICA. CAPRI, FOOT OF MT. SOLARO, 130 M. ELEV. BERGEN (1903). Plot B is a close, dense thicket, 1 to 2.5 m. high. 1732 plants on 100 sq. m. *Arbutus* (464 indivs.), *Pistacia lentiscus* (44), *Q. ilex* (12), *Q. aegilops* (12), *Erica arborea* (12), *Rhamnus alaternus* (12), *Myrtus communis* (124), *Coronilla emerus* (812), *Smilax aspera* (200). 12 spp. on 24.71 mlc.

ERICA MULTIFLORA–GENISTA–ROSMARINUS: SOUTHERN FRANCE. RAUNKIAER (1916: 234, TABLE 3). Raunkiaer designates this, *Erica multiflora* formation. The results in Table 9 are for the bush phase of this vegetation, which includes also a grassland phase. A description, and results for the grass phase and for the vegetation as a whole, will be found in the later section on vegetation-complexes.

MYRTUS, ETC. POZZUOLI, SOLFATARA HILL, S. E. SLOPE, 120 M. ELEV. BERGEN (1903). 1460 plants in 10 spp. on 100 sq. m. *M. communis* (1000 ± 200 indivs.), *Cistus salviaefolius* (190), *Calycotome* (143), *E. arborea* (42), *Spartium* (33), *Q. pubescens* (13), *Q. ilex* var. (10). This is Bergen's Plot C.

SPARTIUM–CISTUS, ETC. CAPRI, N. W. SLOPE, 350 M. ELEV. BERGEN (1903). Plot A, 100 sq. m., 732 plants of 9 spp. *S. junceum* (106), *Cistus villosus* and *C. salviaefolius* (603), *Myrtus* (15), *Daphne Gnidium* (4), *Pistacia, E. arborea, Olea europea,* and *Q. pubescens* (1 each). Near, but not in plot:

Cytisus spinescens ramosissimus, Euphorbia spinosa, Satureia montana, Pinus halepensis.

On Monte Gauro, w. slope, ca. 190 m. elev., Bergen described Plot D with only 2 species, *Colutea arborescens* and *Spartium*. Near D in scanty soil, exposed to full sun, was Plot G, in a vegetation almost wholly composed of *Pistacia* and *Calycotome*. At a lower level was a considerable tract of saplings of *Castanea sativa,* with *Cytisus* (probably *C. scoparius*). These are like the simpler communities of chaparral or bush in California, in which one species, as *Adenostoma* or *Q. durata* or *Ceanothus cuneatus,* dominates, with only a few individuals per acre of any other shrub species.

Thymus, etc., 2 km. e. of Lerida, n. e. Spain. Raunkiaer (1916:233). *T. hiemalis* seems to be strongly dominant, occurring in all 50 of Raunkiaer's plots, whereas none of the 6 other species occurs in more than 4. These include: *Teucrium polium, Helianthemum hirtum, Santolina chamaecyparissus,* and *Genista scorpius.* Effective plot-size for this *tomillar* is est. at .3 sq. m.; spp. per plot, 1.24; one-piece equiv. area 6.41 mlc. The reference areas are relatively large, for the same reason as with the bush near Mt. Lowe: nearly exclusive occupation by the dominant.

NORTH-EUROPEAN HEATH AND DWARF-SHRUB VEGETATION

The resemblance between west-Mediterranean shrub types, which include actual heaths, to the heaths and ericaceous dwarf-shrub communities of western and northern Europe, and the transitions to Arctic dwarf-shrub, have been pointed out by European plant geographers. The descriptions most readily available for the present treatment are those by Raunkiaer, Du Rietz, and Vahl.

Many species that are characteristic and dominant in these shrubby plant covers enter into the field-layer of open forests, and are components in some of the phytocenoses of North-European bogs. These species will again be encountered in the treatments of these vegetation-types.

Table 10. North-European Heath and Dwarf-Shrub.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Nackte *Calluna,* Insel Jungfrun	103.2	418	8.02	12.0	2
Calluna—Hylocomium Heide, Komosse	29.2	118	13.0	18.9	3
Calluna (no. 17) at Østerhede	22.0	89.0	2.50	3.66	3
Calluna—Arctostaphylos, Tinghede	28.5	115	9.88	14.3	3
Empetrum—Hylocomium, Torne Lappmark	61.7	250	11.0	15.9	2
Empetrum—Stereocaulon, Scand. Mts.	35.9	145	10.8	15.7	2
Dryas heath, Njulja, Lapland	21.3	86.3	11.7	16.9	3
Vaccinium—Dryas heath, Njulja	14.9	60.4	19.0	27.9	3

Nackte Calluna Heide, Jungfrun. G. E. Du Rietz (1921: 158). "*Nackte*" describes the nearly bare ground surface (from scarcity of mosses

and lichens). It suggests poor site quality. This widely occurring heath type is of special importance in the Skärgarden or groups of rocky islands of south Sweden. No other plant approaches *Calluna vulgaris,* common heather or ling, in abundance. Other woody plants are *Vaccinium myrtillus, V. vitis-idaea;* dwarfed *Populus alba* and *Sorbus; Empetrum. Melampyrum pratense, Hieracium umbellatum,* and *Deschampsia flexuosa* occur in 38 down to 13 per cent of the quadrats. Species are listed for quadrats of 4 sizes, .01, 1, 4, and 16 sq. m. (effective plot-sizes est. as .03, .3, 1.06, and 4 mlc.). The numbers of quadrats of the 4 sizes are 1000, 100, 20, and 8. The plots are separated, are probably not confined to one stand, but all seem to be taken within a limited district in stands all of one rather closely defined type. 13 spp. in all occur in these plots. Spp. per plot: 1.06, 2.0, 2.5, 3.1. These species-numbers closely locate lower part of species-area curve; upper part is less dependable.

Calluna–Hylocomium Heide, Komosse, Smålandische Hochland. Du Rietz, Osvald, Fries, and Tengwall (1920: 7). The rather rich ground layer of microphytes is not included in the species-count. 25 1-sq.-m. quadrats (effective size .3 mlc.); 7.72 spp. per plot; one-piece equivalent area 12.8 mlc., with 16 spp.

Calluna in sterile flat at Østerhede, W. Jutland. Raunkiaer (1910: 116, Column 17 in Table 36). 50 0.1-sq.-m. plots. *Calluna* in 50 plots, *Empetrum nigrum* in 6, *Carex panicea* in 18. No other species listed. Effective plot-size is est. at .4 sq. m., with 1.48 spp.; one-piece equiv. area, 8.58 mlc. Locality is between Lønborg and Lyhne. Very low and sparse ling vegetation.

Calluna–Arctostaphylos heath, Tinghede. Raunkiaer (1910: 114-115, Column 12 in Table 35). "Højt Terraen vest for Tinghøjene paa Tinghede. Forunden Lyng og Rensdyrlav kun *Arctostaphylos* dominerende: *Calluna–Arctostaphylos* Facies." 11 spp. 2.48 spp. per plot. One-piece equiv. area, 8.58 mlc.

Raunkiaer gives on pp. 114-121 data for many heath types or variants. *Myrica, Erica, Calluna, Empetrum,* and *Arctostaphylos uva-ursi* are dominants in various combinations. The last 3 species dominate in localities summarized in columns 8 to 11 of Table 35, with *Calluna* in 48 to 50 plots in each. Numbers of spp. per plot in these 4 localities are 1.94, 2.16, 2.82, and 2.62. Totals of species listed: 5, 5, 8, and 6. No. 12 is therefore a heath rich in species; no. 17 is very poor in species.

Empetrum–Hylocomium type, Torne Lappmark. Du Rietz (1921 : 159-160). *Empetrum* with ground layer rich in mosses is abundant in the Scandinavian mountains, and in the Skärgården. Du Rietz and his associates studied this heath on Mts. Luopahta and Nakerivaara. He lists the mosses and lichens on p. 159, but omits them from the field-layer species count (Table 13, p. 160). Plot-sizes are 1, 4, and 16 sq. m. In all of the large plots occur *Betula nana,*

Empetrum, Linnaea, Vaccinium vitis-idaea, and *Calamagrostis lapponica.* Other species of note: *Rubus chamaemorus, Salix glauca, V. uliginosum, Cornus suecica, Arctostaphylos alpina.* Spp. per plot in the 3 sizes: 8.01, 8.88, 9.50. Total spp., 17. Effective plot-sizes .3, 1.06, 4 mlc. Equiv. largest area, 95 mlc.

Empetrum–Stereocaulon paschale type. Du Rietz (1921: 155, 157, Table 7). Predominant vegetation in continental mountain districts of northern Scandinavia. Du Rietz studied it in lower alpine zone of the same two mountains, which are on the south side of the eastern part of Torneträsk. 40 1-sq.-m. and 10 4-sq.-m. plots. 4.52 and 5.90 spp. per plot. Total spp. 14. Equiv. total area, 18.6 mlc. Most frequent spp.: *Empetrum, V. vitis-idaea, Betula, Calamagrostis, V. uliginosum.*

Dryas heath, Njulja, Swedish Lapland. M. Vahl (1913: 12-13; Table 7, Column A). Vahl includes this type among "Formations above the limit of the birches." He describes 2 variants on the western declivity of Njulja above Björkliden. It occurs in deep raw humus. *Dryas octopetala, Salix reticulata, Cassiope tetragona, Arctostaphylos alpina,* and *V. uliginosum* are the common dwarf-shrubs. A few other plants are frequent. 50 0.1-sq.-m. plots, effective size .4 sq. m., with 5.28 spp. per plot. 14 spp. in all, on one-piece equiv. area est. at 8.58 mlc.

Vaccinium–Dryas heath with herbs, Njulja. Vahl (1913: 12-13; Table 7, Column B). This has *V. vitis-idaea* in 43 of 50 plots, *V. uliginosum* in 42, *Empetrum* 32, *Cassiope* 23, *Dryas* 21. Herbs and grasses are numerous. Spp. per plot, 8.50; 25 spp. in all.

Du Rietz et al (1920: 7) give a summary of Tengwall's study of moss-rich *Dryas* heath at Nuolja. 54 spp. occur in 15 4-sq.-m. quadrats. Spp. per plot, 28.33. It is not stated whether the count includes mosses and lichens.

In reviewing the characteristics of these heath communities, including the figures of Table 10, one sees a wide range of variation in richness of composition. Very low site qualities with fewest species mark two of the *Calluna* stations. The opposite extreme is the herb-rich *Vaccinium–Dryas* community, which may be regarded as transitional between heath and grassland. Its reference areas are larger than those for most grasslands, smaller than for most heaths. Before much can be said about those communities which have only one to three species in the size of sample ordinarily studied, such as Raunkiaer's *Calluna* at *Østerhede,* additional field studies should be made. In this case the values for reference areas are very uncertain.

Although such impoverished types of vegetation can occur in any latitude with extreme exposure or poorest soil, it may not have been expected that notably rich heaths would be found above the Arctic Circle and at considerable altitude, as on Mt. Njulja.

SHRUB AND BUSH OF ROCKY MOUNTAINS AND GREAT BASIN

The few types here treated make too fragmentary a sample of west-American shrub vegetation, but cannot well be included with any other group. Ramaley's descriptions of communities in the San Luis Valley of southern Colorado deal with types best represented in the Great Basin, but occurring elsewhere in the west.

TABLE 11. Shrub and Bush in Colorado.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	N1000	D
Woody species, Boulder mesa	198.1	801	9.89	15.1	—	1
Sagebrush, San Luis Valley	44.7	181	3.56	5.30	3400	3
Chrysothamnus—Gutierrezia, V. G.	27.0	109	3.93	5.73	4673	3
Sarcobatus—Chrysothamnus, M.	19.2	77.7	2.00	3.17	798	2
Sarcobatus—Chrysothamnus, S. L. V.	46.0	186	2.60	3.78	2252	3

WOODY SPECIES IN MIXED VEGETATION OF ROCKY MESA-TOP ABOVE BOULDER. VESTAL, SEPTEMBER, 1944. This vegetation includes a very few stunted or young conifers scattered among shrubs and patches of inceptive grassland near the boulder-strewn edge of one of the high terraces flanking the outer mountain slope overlooking Boulder, Colorado. For description see the later section on mixed vegetation.

SAGEBRUSH, SAN LUIS VALLEY. F. RAMALEY (1942: 264, TABLE 8). This large intermont plain is in its northern part a basin with no exterior drainage. Its southwestern part is traversed by the Rio Grande. The bottom of the basin is mostly covered by greasewood. Sagebrush, and a more xeric bush–grass mixture of *Chrysothamnus, Gutierrezia,* and *Bouteloua,* occupy wide borders around the saline flats. *Artemisia tridentata* (At) dominates the finer-soiled, less xeric, areas. Its bushes are usually about 2 ft. high; each covers an estimated 7 sq. ft. on the average. With somewhat smaller plants of other species, one may expect to find about 3400 bushes per acre. Ground-space per bush is thus 0.294 mlc. Bushes cover a little more than half the surface. — At four different locations between Fort Garland and San Luis, Ramaley listed bush species in 50 0.1-sq.-m. plots. In all 200 plots, At was represented by 136 bushes or clumps, *Gutierrezia diversifolia* or snakeweed (Gd) by 49, the first of several small-bush spp. of *Chrysothamnus* or rabbitbrush (C-1) by 18, and *Opuntia polyacantha* (Op) by 7 clumps. This enumeration determined proportions for leading species. Other bush or shrub species occurring with At may bring the woody-plant list to 15 or 16 species, but most are rare or local. Grasses of 4 or 5 species, and 3 dicot herbs (one is the Colorado rubber plant, *Hymenoxys floribunda*), are also listed in Ramaley's Table 8. — An incidental finding from his listing of bushes in such small plots as 0.1 sq. m. is that the effective plot-size may be 12.5 times the nominal size. Ramaley recorded on 200 plots,

210 bushes or clumps of the 4 woody species mentioned. If the 210 are of average size, each has the average ground-space of 0.294 milacres: the 210 represent aggregate ground-space of 61.78 mlc., = 250 sq. m. Nominal area of 200 plots is 20 sq. m. Effective plot-size is 0.309 mlc. or 1.25 sq. m. — The one-piece area equivalent to an aggregate of 50 plots of this effective size was estimated to be 40.6 mlc. It includes 138 bushes.

To obtain species-numbers at particular areas, a result of an auxiliary study of tree distribution into plots was used. The object had been to find the "number of available individuals per plot" required to make it likely that a species will occur in a plot. If individuals were perfectly dispersed, a density of one plant for each two plots would give equal chances that the species would or would not occur in a particular plot. Since individuals are not so dispersed, the density which does give 50% probability of occurrence was found by observation for 4 tree species over a range of plot-sizes from that of Ar (smallest representative area, or 0.2 Am) down to $\frac{1}{64}$ Ar. For an irregularly distributed species, a density of 0.88 individuals per plot was found to give 50% probability of occurrence. Thus if a number of plots are of such size that the available population for each assures the presence of 4 species with possibility of a fifth, and with the fifth or least numerous species represented by 0.88 individuals per plot, then half the plots will have 4 species, the others will have 5: average species-number is 4.5. —Areas at which species-numbers are successively 7.5, 6.5, 5.5, . . . 2.5 were found by partly graphic, partly trial-and-error applications of the hollow-curve principle. The likely proportions for numbers of individuals of 4 minor species were found by extending a J-shaped curve determined by proportions for the 4 leading species. The population to go with a particular species-number was found by fixing the number for the least numerous species at 0.88 and proportioning numbers for other species to that one. Area for that population was found by means of the known ground-space per bush (0.294 mlc.). Results for all sizes of area are best shown in tabular form. Figures in the body of the table are numbers of individual bushes or clumps. The middle row of figures is the basis for all the others. — Incidentally, we see that for that row, i.e., for

TABLE 11a. Sagebrush: Populations and Areas at Particular Species-Numbers.

Species No. of spp.	At	Gd	C-1	Op	5th	6th	7th	8th	Population	Area, *mlc.*
7.5	3024	540.4	198.5	76	30	12	4	.88	3885.8	1142
6.5	332.7	119.0	43.7	16.7	6.6	2.7	.88		522.3	153.6
5.5	110.9	39.7	14.6	5.6	2.2	.88			173.9	51.2
4 +	89.5	32.0	11.75	4.5	?				137.75	40.6
4.5	44.4	15.9	5.8	2.3	.88				69.3	20.4
3.5	17.5	6.3	2.3	.88					27.0	8.0
2.5	6.7	2.4	.88						9.98	2.9

The species-area curve, based on figures in first and last columns, gives the Am-value 44.7 mlc. This is a little larger than the one-piece area equivalent to a set of 50 of Ramaley's plots.

the area equivalent to an average set of 50 small plots as observed by Ramaley, the number of bush species that he lists should be interpreted, not as "4," but as "between 4 and 5." The same degree of uncertainty usually applies to any species-number observed on a plot or tract.

Sagebrush in its extensive stands in the Great Basin and in mountain areas bordering it, has different associates, different sizes and spacings, and consequently different species-area relations, from those in the San Luis Valley.

CHRYSOTHAMNUS–GUTIERREZIA BUSH, SAN LUIS VALLEY. RAMALEY (1942: 260, TABLES 5-7). This is part of a bush–grass mixture treated in detail in the later section on mixed vegetation. Stands of this rabbitbrush–snakeweed type commonly adjoin areas of sagebrush and include mostly the same species. It is more xeric than sagebrush, is usually in coarser soil, has higher proportion of surface occupied by grasses and xeric herbs. There is likewise more bare soil, and the bushes are smaller and more widely spaced.

SARCOBATUS–CHRYSOTHAMNUS BUSH, CA. 4 MILES S.W. OF MOSCA, SAN LUIS VALLEY. RAMALEY (1942: 342). 10 plots, each 3200 sq. ft. (40 × 80 ft.). 7 spp. in all: *S. vermiculatus* (greasewood), *Chrysothamnus* (2 spp.), *Atriplex canescens, Sporobolus cryptandrus, Distichlis stricta, Lepidium alyssoides*. Only 4 species are bushes. Density is low, > 80% of the surface being bare. This community was studied by random spotting of plants in a hypothetical area of the extent given (assuming plots to be contiguous). For each species, individuals in the correct number were located in the manner earlier described. By subdividing plots and finding average species-number for each of 9 sizes of plot, figures for a species-area curve were obtained. They ran, in part, .908 spp. per 50-sq.-ft. plot, 2.15 spp. in 200 sq. ft., 3.15 in 800, 3.8 in 3200, 4 spp. in 6400 sq. ft., and no more than 4 in each larger size up to the total of 32,000 sq. ft. It may be possible that a very much larger area than Ramaley recorded would have the same 4 bush species and no others. This result might be expected if the site excludes most bush species of the district. A more extreme condition may be present in the fine-textured, saline, at times flooded or waterlogged soils of many playas of the Great Basin. Some of these may be habitable only to greasewood. A truly pure stand of one species exhibits the minimum in floristic richness. In the San Luis Valley, some greasewood areas have less extreme environments than the one with 4 species, as Ramaley's second greasewood example shows.

SARCOBATUS–CHRYSOTHAMNUS, 20 LOCATIONS. RAMALEY (1942: 244, TABLE 2). In each of 20 places in the San Luis Valley, Ramaley listed species in 50 0.1-sq.-m. plots. *Sarcobatus* occurs in 440 plots, *Chrysothamnus* in 360, *Atriplex canescens* in 11, *Franseria acanthocarpa* 9, *Gutierrezia* 9, *Senecio spartioides* 7. Ramaley did not separate the different species of rabbitbrush, but mentions that there are more than 6 of them. For species-area treatment, the

360 plots with some species of *Chrysothamnus* are arbitrarily divided among 5 species thus: 234, 86, 21, 13, 6. Excluding herb species in his table, bush species occur in 836 of the 1000 plots, making the number of bush species per plot 0.836. Assuming a total of 900 bushes, with 1 bush covering 5.8 sq. ft. and with bushes occupying 30% of the surface, then 900 bushes occur in 400 mlc., an acre contains 2252 bushes, and 100 bushes occupy 44.4 mlc., with 3.77 spp. (this species-number from a trial section of a species-area graph). By C-conversion from 100 bushes with 3.77 spp., 20 bushes on 8.88 mlc. include 2.57 spp.; 5 bushes on 2.22 mlc. include 1.67 spp. — Unlike the preceding example, this one shows very slow but continuous increase of species with area, with a presumed 6.5 species at 10 acres, 8.2 at 1000 acres (as read from the extended species-area curve). Ramaley's 1000 plots in 20 places with 10 bush species thus sample a very large area, perhaps equivalent to a uniform stand of 5 to 15 square miles.

GRASSLANDS

TABLE 12. Tall-Grass Prairies, and Sand Prairie.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Mesophytic prairie, n.e. Ill.	17.0	68.8	24.7	35.5	3
Af—As facies, Nebraska City, Neb.	6.33	25.6	47.7	68.6	3
As—Af facies, Nebraska City	8.64	35.0	42.5	61.3	2
High prairie near Lincoln, Neb.	6.89	27.9	28.2	42.0	1
Low prairie near Lincoln	7.90	32.0	35.2	53.2	1
Sporobolus—Andropogon, N. D.	14.3	57.9	62.0	89.3	3
A. scoparius type, N. D.	12.0	48.6	36.0	52.2	3
Eragrostis, etc., Havana, Ill.	18.5	74.7	12.7	18.1	1
Pastured bunch grass, Havana	44.3	179.4	17.5	25.9	1
Leptoloma variant, Oquawka	15.0	60.7	17.1	25.3	2
Interdunal flat, Hanover	24.0	97.1	23.9	34.8	3
Lower slope, Hanover	27.6	116.9	22.1	32.9	2
Upper slope, Hanover	18.4	74.6	22.3	32.4	2
Plateau-top, Hanover	70.0	283.1	22.9	33.2	2
Sparse vegetation, blowsand	75.0	303.3	5.59	8.34	3
Calamovilfa type, N. D.	13.0	52.4	30.0	43.0	3

MESOPHYTIC PRAIRIE NEAR ELMHURST, N.E. ILLINOIS. VESTAL (1913: 357). A small relict area of good prairie, including large bunches of *Sporobolus heterolepis,* was preserved in an acute angle between two intersecting railroads, not far west of Chicago. Prairie of this district is characteristic of the fertile dark soils of late Wisconsin glaciation. This area had 35 spp. in 20.66 mlc. A larger area estimated at 70.66 acres, had 80 spp. It includes some variations of site, chiefly dependent on small differences of level and drainage, but species found only in lower spots were excluded from the list. As seen in Table 12, reference areas are larger and species-numbers are smaller than for prairies farther west. One should not infer from this single example that eastern prairies show more severe competition than those in the middle of the prairie region, nor that the eastern prairie flora is more limited.

ANDROPOGON FURCATUS–A. SCOPARIUS FACIES, NEAR NEBRASKA CITY, NEB. J. J. THORNBER (1901). This early statistical study is still of highest value. The map permits estimates of the larger areas; numerous detailed enumerations for 1-sq.-m. quadrats are given. Only 4 plots are reported for this less xeric type, with the taller bluestem the leading dominant. Plot no. 6, east slope, and nos. 4 and 7, north slope, have the 2 *Andropogons* as dominants. No. 5, west slope, also has *Panicum virgatum*. In general, little correlation is evident between exposure and type, or between exposure and no. of spp. For these 4 plots, there are 29 to 38 spp. (38 in the Af–As–Pv plot, no. 5). Mean species-number is 32.75. The trend of the curve for this facies was judged from that for the As–Af type, next mentioned.

A. SCOPARIUS–A. FURCATUS FACIES. THORNBER (1901). This facies has 2 dominants, little bluestem in the lead. There are 8 quadrats, with 25 to 32 spp.; mean is 27.5. The plots are in various exposures and levels. Lower part of curve was based on species-numbers for smaller areas than 1 sq. m., found by means of no. of individuals in Quadrat 1, using C-conversion. Upper part was based on total of 141 spp. in 155.4 acres of typical prairie (est. from Thornber's map).

A group of types, in some respects intermediate between the drier As–Af and the less extensive Af–As facies, has the same 2 dominants plus one other. Of 10 such quadrats 3 are As–Af–Bc (*Bouteloua curtipendula*), 1 is Bc–As–Af, 2 have *Panicum Scribnerianum* as the third dominant, 2 have *Koeleria cristata*, 2 have *Carex pennsylvanica*. Species-numbers, 27 to 35; mean is 29.5. If these 10 quadrats were considered as representing one type, reference areas and species-numbers on a curve would surely fall between those for the two types just given.

HIGH PRAIRIE NEAR LINCOLN, NEBRASKA. T. L. STEIGER (1930). This comprehensive presentation of plot data for two types of prairie is an outstanding example of the great usefulness of field data when published in detail. It has already been the subject of statistical treatments by several investigators. In 40 1-sq.-m. quadrats in high prairie, Steiger recorded 43 + 2 species (17 grasses, 28 other herbs). Spp. per plot, ca. 17.4. In a total of several hundred acres. Steiger listed 81 species (excluding the introduced ruderals); 70 of the 81 species are characteristic of high prairie. By different combinations of the 40 plots, mean species-numbers were obtained for 3 other plot sizes: 32.4 spp. in 5 sq. m., 38.8 in 10 sq. m., 48.5 in 20 sq. m. Thus a dependable basis for a curve is assured. — The plot data include counts of individual plants. Thus in 1 sq. m., mean no. of grass individuals is 218; of other herbs is 32.2. This is 6.2 sq. inches per plant or 40 sq. cm., or 0.0430 sq. ft.

LOW PRAIRIE NEAR LINCOLN. STEIGER (1930). The article gives similar data for 40 quadrats in low prairie, with 56 species; and with a total of 75 species in a general area considerably smaller than that for high prairie. These 75

species also do not include ruderals. 45 of the 75 are characteristic of low prairie; 20 do not occur in the high-prairie area. Mean no. of spp. is 18 in 1 sq. m., 32.4 in 5 sq. m., 38.8 in 10, 48.5 in 20. — Individuals are smaller and herbage is denser in low prairie. Per sq. m., mean no. of grasses is 270.55; of other herbs is 53.3. Ground-space per plant is 4.8 sq. inches, or 31 sq. cm., or 0.0333 sq. ft.

The one Illinois and two Nebraska localities show conclusively one important feature of at least these species-area curves, since each affords a species-number for a large area, 70 to several hundred acres, or *4000* to *58,000* times the minimum area. A curve for any of these localities, if extended to so large an area, convincingly demonstrates that the upper section of a species-area curve cannot have so steep a slope as the middle section. If, for example, the curve for Steiger's high prairie continued at the slope of its steeper middle section as far as 300 acres, the indicated number of species would be 137. Steiger's tally for the whole high-prairie area studied (estimated as 400 acres, possibly no more than 300) is 81. It is inescapable, therefore, that the large-area section of such a curve is convex, with progressive decline in slope at all points beyond the point of flexure. This has been found true in all cases for which large-area tallies are available.

Sporobolus heterolepis–Andropogon furcatus prairie, western North Dakota. H. C. Hanson and W. Whitman (1938). For each of ten types of prairie vegetation, the authors selected a number of representative test areas, with homogeneity a chief requirement. There are 36 of these test areas, each of 2 to 20 acres. In each test area Hanson and Whitman established 30 scattered 1-sq.-m. quadrats. The average number of species per plot in the 30 plots or quadrats, and the total number of species in the 30 plots, are given for each of the different test areas as part of their Table 1 on page 61.

One test area in each of six of their types was used in the present species-area study. Of 4 localities for the *Andropogon furcatus* type, test area 30 was selected. The type is richer in species than others, and this *Sporobolus–Andropogon* variant in area 30 is richest within the type. It has 86 spp. in the 30 scattered quadrats, and a mean of 20.3 spp. per quadrat. The area is ca. 16 miles n. of Kildeer, near the edge of the "breaks" of Little Missouri River, on lower part of a gentle north slope. Soil is a dark-colored fine sandy loam. The authors considered it the best-developed prairie they studied. The present writer's experience with eastern prairies led him to regard *Sporobolus heterolepis* as an indicator of least disturbed prairie, usually in favorable sites. The best early description of Illinois prairie, by C. W. Short (1845: 191) includes a mention of *Vilfa heterolepis* conveying a similar impression; it is the species most palatable to grazing animals: first to be "eaten out." In addition to this grass and the big bluestem, one or more small xeric grassland species of *Carex, Stipa comata,* and *Calamovilfa* are dominant. — The curve is based on 3 points, one for species-number at .247 mlc. (20.3 spp.); a second point for a one-piece area equal to the aggregate of 30 plots (30 sq. m. or 7.41 mlc., with an estimated 79 spp.);

the third point is for the one-piece area which will include the number of species (86) given for the 30 scattered plots (this area is est. at 11.76 mlc.). Species-numbers for these same three areas are similarly used for each of the other 5 types borrowed from Hanson and Whitman.

Andropogon scoparius type, North Dakota. Hanson and Whitman (1938). Test areas 25 and 26 are of this type. The former is on the lower part of a 20-to-25-degree slope, with dark-brown, fine sandy loam of high carbonate content, on the Olstad Ranch ca. 16 miles s.e. of Sentinel Butte. Spp. per plot, 12.8. 52 spp. in 30 scattered plots or in a one-piece area of 11.76 mlc.

Bunch-grass of sand prairie: Eragrostis–Leptoloma–Panicum variant, Illinois River dunes. H. A. Gleason (1907: 160, Table 1). Some of the more extensive eastern sand prairies are in the dunes of widened parts of major river valleys, just below terminal moraines of the Wisconsin ice-sheet. Gravels and sands were deposited by the glacial torrents over what now are extensive terraces. Dunes of the Illinois River were studied by Hart and Gleason (1907). Of Gleason's quadrat studies in sand prairie near Havana, Du Rietz wrote (1924: 430, after a paragraph on "Die rein technische Quadrat methode"): "Zu wirklich statistischen Untersuchungen wurde die Quadrat methode wahrscheinlich zum ersten Mal von Gleason (Hart und Gleason 1907, vergl. Du Rietz 1921 p. 102) verwendet; auch in dieser Hinsicht enthält also die Arbeit RAUNKIAERS von 1909 nichts Neues." — Gleason's earlier quadrats are of generous size, 100 square feet. Tables give details for each individual quadrat, and include abundance data which permit one to find approximate numbers of individuals per quadrat. Abundance classes (with specified limiting numbers) are indicated by symbols for particular species in each plot. — The bunch-grass type in Table 1 is dominated by *Eragrostis trichodes, Leptoloma cognatum,* and *Panicum* species. The area is a strip 110 × 10 ft., of 11 quadrats, with 20 spp. in all. The area of a compact plot (a square) which includes 20 spp. was estimated to be 1500 sq. ft., or 34.4 mlc. One quadrat has 9 to 14 spp.; mean number is 11.09. For small areas, Plot 2 with 11 spp. was "mapped" by random spotting of the proper number of individuals for each sp., and divided into quarter-plots. Arrangements of adjacent whole plots in groups of 2, 3, and 5 brought the number of plot-sizes to 8. The curve fitted to the 8 points has lowest rate of increase among 8 curves for bunch-grass vegetation in sand.

Pastured bunch-grass, Havana area. Gleason (1907: 161, Table 2). No cattle had been on the area during two years preceding Gleason's field study. Dominant grasses were *Bouteloua hirsuta, Paspalum setaceum,* and *Panicum* sp. In a 10-plot strip (100 by 10 ft.), 24 spp. were recorded. Equivalent compact area is 31 mlc. Spp. per plot, 12.2. Curve is based on 5 plot-sizes.

Leptoloma variant, Oquawka area, Mississippi River dunes. Gleason (1910: 62, Table 1). For his second article on the vegetation of sand areas in

U. OF ILL. LIB.

Illinois, two tracts of dunes along the Mississippi were among those studied. The Hanover area is not far from the northwest corner of the state. The Oquawka area is perhaps 100 miles farther down-stream. — The *Leptoloma* variant is dominated by an eastern bunch-grass allied to *Panicum, L. cognatum.* It is green and leafy, low, and in places almost turf-forming. It has bright-red fine-branched panicles which break off and roll with the wind as tumble-weeds do. It has in many places become dominant along roadsides in sand, and tolerates disturbance of several kinds. In a stand of this grass Gleason listed species in a strip of 10 quadrats, each 2 m. square. 25 spp. in all; 10.6 spp. per plot; 5 sizes of plots or aggregates. *Paspalum* and *Bouteloua, Ruellia ciliosa, Baptisia bracteata, Ambrosia psilostachya,* and *Monarda punctata* are notable in the list. This and most of Gleason's later enumerations were frequency data: for each column representing a quadrat, occurrence was noted for each species present by a symbol.

Mixed bunch-grass, interdunal flat, Hanover area. Gleason (1910: 66-67). In a series of sites beginning southwest of the Hanover railroad station, Gleason studied variations of mixed bunch-grass in different slopes and levels. The densest vegetation was in a flat area between dunes. Since in this area as well as the others, more than 2 or 3 bunch-grass species were important, Gleason named this type the mixed consocies.* The 8 bunch-grasses and 1 sedge of the flat include two dominants, *Leptoloma* and *Koeleria,* which occupy more space than all the others (*Stipa spartea, Sorghastrum,* 3 species of *Panicum, Carex Muhlenbergii,* and *B. hirsuta.* Other notable plants are *Selaginella rupestris, Callirrhoe triangulata,* and *Tephrosia virginiana.* A census of 10 plots, each 2 m. square, was made. Gleason recorded 29 species in the plots, 11 others outside. — Compact area to yield 40 spp. is est. at 58 mlc. Mean species-number per plot of .988 mlc. is 12.1. The curve for this interdunal flat shows fewer species at small areas than does the upper part of the slope beyond the flat, but probably more species at sizable areas.

Mixed bunch-grass, lower slope, Hanover. Gleason (1910: 69, Table 2a). Through the slope beyond the flat, Gleason surveyed a line of 20 plots in the lower part and 20 plots in the upper part. Each plot is 0.5 meter square. In the lower part, bare-sand spaces between grass bunches were small. *Leptoloma, Panicum pseudopubescens, P. perlongum,* and *Koeleria* are the dominants. *Andropogon scoparius, Sorghastrum,* and *Callirrhoe* are among the other plants. Species per ¼ sq.-m. plot, 2.5. In all 20 plots, 14 spp. 3 intermediate plot-sizes.

* In both 1907 and 1910 articles, a variant or facies of some plant association, characterized by some one or a few dominants, was designated a *consocies.* This was in the period before Clements had narrowed the meaning of this term by associating the ending -ies with temporary status in a succession, and before the erroneous idea had become wide-spread that a consocies in the original sense or its later equivalent *consociation* could have only one dominant. Ecologists should take note of the original signification of consocies, which was the generally understood meaning before about 1920.

Mixed bunch-grass, upper slope, Hanover. Gleason (1910: 69, Table 2B). Here the vegetation is more open, interspaces are larger, leaving more room for interstitial annuals and other plants which do not compete well with the bunch-grasses. The effect is to increase no. of spp.: av. per plot, 4.3 spp.; in all 20 small plots, 16; frequencies of occurrence-in-plots of all species except *Leptoloma* are higher. Dominants are *Leptoloma, B. hirsuta, A. scoparius, Koeleria, P. pseudopubescens. Aster linariifolius* is frequent. *Talinum rugospermum* is in 1 plot. 6 plot-sizes.

Mixed bunch-grass, plateau-top, Hanover. Gleason (1910: 70). On the elevated surface beyond the slope, 10 plots, each of 4? sq. m. Spp. per plot, 9.4. 22 spp. in the plots; 14 other spp. outside the plots. Estimate of area examined (with 36 species), is 110 milacres. Species-numbers at a given area on this upland are smaller, and reference areas are larger, than for other sites in the mixed consocies. The reference areas are smallest in the upper-slope site, perhaps because there is less competition there than there is in other locations.

Sparse vegetation of blow-sand, Havana area. Gleason (1907: 166-167, Tables 5-7). These tables give the plant census for three typical areas of blow-sand, which is nearly bare, with surface drift of wind-blown particles and usually very sparse cover of annuals, as *Cassia chamaecrista, Cenchrus, Commelina,* the rare viscid herb *Cristatella Jamesii,* and of scattered or locally abundant shoots of *Ambrosia psilostachya,* from its rhizomes an inch or two below the surface. In each area 5 quadrats, each 10 ft. square, were recorded. The composite data served as basis for species-numbers for 6 plot-sizes. Numbers of spp. in the 3 groups of plots: 5, 7, 4; in all 3 groups, 8. Spp. per 100 sq. ft, 2.93. Estimated compact area to include 8 spp., 52 milacres.

Calamovilfa type, North Dakota. Hanson and Whitman (1938: 78-80, 94). *C. longifolia* is a tall coarse-textured bunch-grass distinctive of sand (either loose, or stabilized somewhat loamy sand). It is chiefly found in sand prairie, as in sandy plains east of Denver. In North Dakota it "occurs widely on sandy ridges and hills"; it is frequent in the river dunes of Illinois. It is also widely distributed along sandy upper beaches of Lake Michigan and Lake Huron. Hanson and Whitman record it as a distinctive prairie type, giving records from Test Areas 21 to 24: 35 to 42 spp. in 30 1-sq.-m. quadrats, with 9.9 to 12.6 spp. per quadrat. A curve was drawn for Area 21, richest in species of the four. It is on a sandy upland ridge on Olstad Ranch, ca. 16 miles southeast of Sentinel Butte. Soil is fine sand to sandy loam. Other plants are *Andropogon Hallii,* a bunch-grass also characteristic of sand, *Meriolix, Yucca glauca.* One-piece area equiv. to 30 scattered quadrats (as in other cases) is est. at 11.75 mlc.

TABLE 13. Grasslands of Great Plains and Mountain Border

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Bouteloua—Stipa—Carex type, N. D.	16.2	65.6	32.5	46.8	3
Agropyron—Bouteloua—Carex type, N. D.	1.10	4.45	9.95	14.3	3
Plains near Browning, Montana	2.26	9.15	14.2	20.5	3
Grassland at Glacier Park, Montana	5.03	20.4	14.1	20.4	3
Meadow near Palmer Lake, Colorado	10.5	42.5	22.2	32.1	3
Mesophytic prairie, Palmer Lake	4.71	19.1	22.4	32.2	3
Short-grass with bushes, near Boulder	7.14	28.9	22.7	34.0	2

BOUTELOUA–STIPA–CAREX TYPE, NORTH DAKOTA. HANSON & WHITMAN (1938: 61, 63-68). This extensive type, No. 1, occupies level or moderately sloping areas, mostly of sandy loams developed from sandstones or from materials eroded from former buttes or hills. *Bouteloua gracilis, Stipa comata,* and a grassland species of *Carex* are the usual dominants. The authors give data for Test Areas 1-3, 4, 6, and 7, with 10.9 to 19.2 spp. per 1-sq.-m. quadrat, and with 33 to 53 spp. in 30 scattered quadrats. Data for Area 6 were used for a curve. No. 6 has 11.5 spp. per plot; 44 spp. in 30 plots. It is on a gentle north slope, 26 miles southwest of Belfield on road to Ranger.

AGROPYRON–BOUTELOUA–CAREX TYPE, NORTH DAKOTA. HANSON & WHITMAN (1938: 69-71). Type 2 is in fine soils, clay loam to clay, on long, gradual slopes. Carbonate accumulations are not far below the surface. Test Areas 10-13 have 3.7 to 11.0 spp. per quadrat, 12 to 29 spp. in 30 plots. Area 10, used for an S-curve, has good representation of all 3 dominants, *A. Smithii, Bouteloua,* and *C. filifolia.* Absence of *Stipa,* which is characteristic of coarse soils, is apparently an indication of this type. Area 10 is 11 miles northeast of Sentinel Butte. It has 10.3 spp. per plot, and 20 spp. in 30 plots.

PLAINS NEAR BROWNING, NORTHWEST MONTANA. VESTAL, JULY, 1914. The reservation of the Blackfeet Indians lies east of the front of the Rocky Mountains and just south of the international boundary. The principal village, Browning, is about 14 miles from the mountains. A few miles north of Browning, plains vegetation at about 3000 feet elevation comprises at least four types: a xeric extreme, moist meadows of low ground, and intermediate grassland (the extensive type), and a hill prairie on south slopes of sizable hills. Presumably this last site has a longer growing season, permitting the presence of Columbia Basin species. In the extensive type the chief grasses are *Agropyron* species, *Koeleria,* and *Stipa comata,* all of reduced stature. *Selaginella densa* and *Artemisia frigida* are in spots abundant, almost dominant. *Carex stenophylla* and a *Sporobolus* occur locally. Other *Artemisias, Astragalus* species, a *Rosa, Penstemon, Gaillardia, Chrysopsis, Lithospermum, Liatris, Sphaeralcea coccinea,* a *Gaura,* and species of *Eriogonum, Solidago,* and *Aster* are notable. — In a plot of 144 square ft., 22 spp. In one acre, an est. 36 spp.

Grassland at Glacier Park, Montana. Vestal. July, 1914. This is practically closed prairie-like grassland, few plants exceeding 12 inches height in the drier, more extensive sites, to 18 inches in less-dry places. The prairie occupies terraces and low rolling hills of the mountain-border. The area most studied was southeast of the railroad station, on the west side of Two Medicine Creek. Grassland alternates with groups of aspen and of lodgepole pine. Los spots and aspen borders include tall-herb species. South slopes show a temperature-variant with more of the Columbia Basin species such as *Balsamorhiza sagittata.* One of these, the bunch-grass *Agropyron spicatum,* is the chief dominant over the general area. Other grasses are *A. violaceum, Koeleria,* and species of *Danthonia, Poa, Bromus,* and *Phleum.* Herbs include species of *Potentilla, Aragallus, Lupinus, Peucedanum, Penstemon, Campanula, Achillea, Erigeron, Eriogonum, Heuchera, Lathyrus, Phlox, Artemisia, Chrysopsis, Agoseris. Selaginella densa* is local.—In 120 sq. ft., 18 spp.; in 1 acre, 35 spp.

Meadow near Palmer Lake, Colorado. Vestal, July, 1913. The divides between major streams running out from the mountains are much higher and receive more rainfall than other parts of the eastern border of the Southern Rocky Mountains. One such high divide is near the Wyoming-Colorado boundary. The next is the Platte-Arkansas divide some 60 miles south of Denver, with Palmer Lake, the station, at its summit. The lava-capped mesas at the New Mexico boundary form the third high divide. Mountain plants, including the conifers, extend far east of the mountains on these divides. At Palmer Lake, (elev. 7237 ft.) the grasslands show several types, including meadow in low ground, a mesophytic mixed prairie in well-drained sites, and patches of mountain bunch-grass in some rocky or gravelly spots on cliffs or tops of buttes. The meadow studied was near the railroad, north of the station. *Phleum pratense* was the abundant grass, with *Poa, Agropyron,* and *Muhlenbergia.* There were also a *Juncus, Sisyrinchium angustifolium,* and *Allium recurvatum;* and numerous dicot herbs, including *Potentilla, Thermopsis, Lathyrus, Rudbeckia, Aster,* and *Achillea.* — A small area of 36 sq. ft. had 17 spp.; a larger area estimated at 324 sq. ft. had 30 spp.

Mesophytic prairie, Palmer Lake, Colorado. Vestal, July, 1913. (For a description of local mountain-border prairies, see Vestal, 1914: 390.) This rather dense grassland was just above the meadow of the preceding paragraph. The dominant grass was *Stipa viridula,* with *Agropyron Smithii, Koeleria,* and a *Bromus. Calochortus gunnisonii, Geranium Parryi, Galium boreale, Lupinus argenteus, Erigeron macranthus,* and species of *Artemisia, Aster, Cirsium, Monarda,* and *Rosa* were conspicuous. — In 60 sq. ft. there were 25 spp., and in 484 sq. ft., 38 spp.

Short-grass with bushes, east of Boulder, Colorado. Vestal, September, 1912. The "bushes" are barely more than suffrutescent herbs. See description in later section on mixed vegetation.

TABLE 14. Mountain and Intermont Grasslands, Colorado.

Stand or type		Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Foothills n.w. of Boulder, 7000 ft.		16.5	56.8	30.3	43.7	3
Upper Arkansas valley, Buena Vista		10.7	43.3	14.8	21.9	3
Mountain park grasslands, Tolland, 8800 ft.						
Erigeron multifidus	ridge	6.31	25.5	22.7	32.9	3
Muhlenbergia—Comandra	slope	10.0	40.5	32.3	46.2	3
Muhlenbergia—Antennaria	slope	6.78	27.4	35.9	51.9	3
Muhlenbergia—Aragallus	slope	6.81	27.6	30.9	44.8	3
Muhlenbergia—Danthonia	less xeric slopes	8.25	33.4	32.2	46.7	3
Grassland of glacial sink		6.08	24.3	35.3	52.0	3

FOOTHILL MIXED GRASSLAND, N.W. OF BOULDER. 7000 FT. ELEV. VESTAL (1917 : 373-375). The station is on an east slope below the top of a round-topped granite hill 2 miles west of the mountain front. Abundant species are *Bouteloua gracilis, Phacelia heterophylla, Chrysopsis, Senecio oblanceolatus, Geranium Parryi, Artemisia frigida, Aragallus Lambertii.* Also notable are *Koeleria, Mertensia lanceolata, Carex pennsylvanica,* and species of *Lesquerella, Linum, Gilia, Helianthus, Eriogonum, Gaillardia,* and *Townsendia.* — 24 spp. in plot 8 × 8 ft. (1.47 mlc.). Est. no. of spp. in one acre, 72.

SUBMONTANE DRY GRASSLAND, INTERMONT PLAIN OF UPPER ARKANSAS VALLEY, AT BUENA VISTA. 7950 FT. ELEV. VESTAL, JUNE, 1914. The area studied is close to the town, west of the river. It is flat, with coarse soil and a few surface rocks. The dominant grass was *Bouteloua gracilis. Artemisia frigida* was abundant, locally dominant. Frequent plants were *Sitanion brevifolium, Hymenoxys floribunda* (Colorado rubber plant), an *Erigeron,* a *Sideranthus,* and small bushes of *Eriogonum effusum.* Numerous less frequent species included *Opuntia polyacantha, Echinocereus viridiflorus, Selaginella densa, Erysimum, Hymenopappus.* — 12 spp. at 48 sq. ft. (1.10 mlc.) ; 27 spp. at ca. 2000 sq. ft. (45.9 mlc.)

This grassland has been modified by grazing, and bears considerable similarity to the grassland with bushes on a rocky mesa-top east of Boulder, described in a later section on mixed vegetation.

MONTANE PARK GRASSLANDS, MIDDLE BOULDER PARK, NEAR TOLLAND. 8800 FT. ELEV. F. RAMALEY (1914, 1915, 1916). Ramaley had in earlier papers briefly described the dry grasslands of the stony floor of this small glaciated plain surrounded by mountains. Meadows in the flood-plain, sedge moors and willow thickets bordering the stream (Middle Boulder Creek), and occasional single trees or conifer groups, are the other kinds of vegetation in the park. In the 1915 article, Ramaley gave details for 16 grassland quadrats, each 1 sq. m., as percentages of cover for single species (or in some cases for 2 or 3 species of one genus). The high variability of composition shows in number of species per

plot: the range is from 9 to 23. It can hardly be said that there is any modal number of species. These species-numbers were used in estimating likely numbers of species per plot for the sections of strips of plots in Ramaley's 1916 paper. In this he described an east-west line of 138 quadrats, with an additional row of 20 plots starting from plot 45 in the main strip. There are six variants, depending on topography and exposure. Data for the six variants do not include details for individual plots. Cover percentage is given for different species, in each variant and in the 158-plot aggregate.

Erigeron multifidus society. On xeric ridge, plots 1-16. Dominants are *Koeleria, Carex stenophylla,* and *Aragallus Lambertii.* Est. mean no. of spp. per plot, 12. 32 spp. in 16 plots. Est. equiv. compact area, 22 sq. m. or 5.44 mlc.

Muhlenbergia–Comandra society. Xeric slope, plots 37-76, 139-158. The most extensive variant. *M. gracilis* and *Comandra pallida; Artemisia frigida,* and *Chrysopsis villosa* are the important species. Spp. per plot, ca. 13. 54 spp. in 60 plots. Est. equiv. compact area, 108 sq. m. or 26.7 mlc.

Muhlenbergia–Antennaria anaphaloides society. Xeric slope, plots 17-31. *Festuca saximontana, Chrysopsis,* and *Cerastium occidentale* are important. Spp. per plot, ca. 19. 49 spp. in 15 plots. Est. equiv. compact area, 20.3 sq. m. or 5.02 mlc.

Muhlenbergia–Aragallus society. Xeric slope, plots 92-110. *M. gracilis* covers 14.8% of area, *Koeleria* 6.7%, *A. Lambertii* 5.4%. *Danthonia Parryi* and *Artemisia* are also important. Spp. per plot, ca. 16. 45 spp. in 19 plots. Est. equiv. compact area, 28 sq. m. or 6.92 mlc.

Muhlenbergia–Danthonia society. On 3 hypoxeric slopes, plots 32-36, 77-91, 127-138. *Festuca saximontana* with 11.9% cover, *D. Parryi* with 6.4%, and *Cerastium* with 3%, are important. Spp. per plot, ca. 15, 57 spp. in 60 plots. Est. equiv. one-piece area, 120 sq. m. or 29.7 mlc.

Danthonia intermedia variant, occupying glacial sink. Plots 111-126. *D. intermedia* has 9.2% cover; *Muhlenbergia gracilis* has 11.8%. Spp. per plot, ca. 18. 50 spp. in 16 plots. Est. equiv. compact area, 22 sq. m. or 5.44 mlc.

COLUMBIA BASIN GRASSLANDS

A distinctive prairie-like formation occupies parts of the northern Great Basin, and of lower to middle elevations of included and bordering mountain ranges, as well as numerous intermont plains of those mountain districts. Infusions of its flora are found in the plains of British Columbia; east through the Rocky Mountains in Montana, Wyoming, and northern Colorado; west of the Cascades as far south as Shasta Valley, and southwest as far as the east slopes of the southern Sierra Nevada. This grassland has less severe winters and drier

summers than Great Plains and prairie grasslands east of the mountains. Absence of species of *Andropogon* and *Bouteloua;* dominance or abundance of *Agropyron spicatum, Festuca* species, *Balsamorhiza, Wyethia,* etc., are characteristic.

TABLE 15. Columbia Basin Grasslands.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Dry prairie, Wild Horse Island, Montana	12.55	50.4	17.5	26.2	3
Openings, Osprey Island, Montana	5.37	21.7	14.2	21.3	3
Agropyron—Poa, Garfield Co., Wash.	0.799	3.15	12.08	17.7	3
Agropyron—Poa, Franklin Co., Wash.	1.255	5.08	11.61	17.1	3
Festuca—Agropyron, Whitman Co., "B"	2.39	9.68	23.7	34.6	2
Festuca—Agropyron, Whitman Co., "A"	4.60	18.6	22.5	32.7	2

DRY PRAIRIE, WILD HORSE ISLAND, FLATHEAD LAKE, N.W. MONTANA. VESTAL, JULY 2, 1914. Grasslands of the northern-Great-Basin type occur on adjacent lands south and west of this large lake, and scatteringly in a narrow thermal belt on the west flank of the Mission Range (east of the lake). Wild Horse Island is several miles long, and is in the large bay on the west side. Dry grass-covered low hills occupy much of its area. Relatively few species occupy the driest high and more exposed sites. Draws and depressions are wet in spring, but are mostly dry by midsummer. In the intermediate sites, to which this description applies, almost all species of the grassland list are found. *Agropyron spicatum* is the chief dominant. *Koeleria,* other *Agropyrons,* and species of *Elymus, Poa, Festuca,* and *Aristida* are relatively infrequent. *Balsamorhiza sagittata* (balsam-root), a *Helianthella,* species of *Lupinus* and of several umbelliferous genera; *Chrysopsis, Artemisia, Erigeron, Achillea, Agoseris, Castilleja, Allium, Zygadenus, Calochortus,* are conspicuous. *Lewisia rediviva* (bitter-root) and *Clarkia pulchella* (appropriately named for the explorers of the northwest) are characteristic. Moderately or less frequent are species of *Eriogonum, Sieversia, Potentilla, Phacelia, Campanula, Antennaria.*—14 spp. in 64 sq. ft. or 1.47 mlc.; 31 spp. in a larger area est. at 1800 sq. ft. or 41.3 mlc.

OPENINGS, OSPREY ISLAND, FLATHEAD LAKE. VESTAL, JUNE 27, 1914. This small island in the south part of the lake was largely forested. There and in forests east of the lake are many openings with mixed herbaceous cover of plants from open forest, meadow, and dry grassland. (Many mesophytic herb species occur equally in meadows and in openings.) Surrounding woody plants are *Pinus ponderosa, Pseudotsuga, Ceanothus, Physocarpus, Symphoricarpos, Ribes.* In two similar and nearby openings: *A. spicatum dominant, Balsamorhiza, Koeleria,* a tall *Poa, Peucedanum* or *Cogswellia, Allium, Erysimum, Penstemon, Berberis aquifolia* (woody at base), *Fragaria,* etc. (In other clearings: *Pteridium, Carex* spp., *Collomia, Clarkia pulchella, Heuchera, Chamaenerion, Antennaria, Vicia, Collinsia, Galium, Hieracium, Castilleja,* etc.)—13 spp. in 36 sq. ft., or .826 mlc.; 24 spp. in ca. 500 sq. ft. or 11.48 mlc.

AGROPYRON SPICATUM–POA SECUNDA ASSOCIATION, S.E. WASHINGTON. R. F. DAUBENMIRE (1942: 64-68). *Agropyron* forms large bunches, 37 to 40 per milacre. There are also occasional large herbs, the small bunchgrass *Poa secunda,* and large numbers of small annuals covering much of the ground between larger plants. This association is developed in a wide belt between the *Artemisia–Agropyron* association of drier plains to the northwest and west and the *Festuca–Agropyron* association of less xeric country closer to the Bitterroot and Blue Mountains. Daubenmire gives descriptions of two undisturbed stands, one near the less xeric eastern edge of the *Agropyron* belt in n. Garfield Co., the other near the xeric western edge in e. Franklin Co. His Table 3 gives frequencies in 100 small plots for each stand. Plots are 2 × 5 dm., arranged in rows with plots separated by 1 meter. From total of occurrences in plots, the mean no. of spp. per plot is 8.57 for Garfield Co. (G), 7.00 for Franklin Co. (F). No. of spp. in 100 plots is 24 in G, 22 in F. The one-piece area equivalent to the plot-aggregate was estimated on the assumption that plot-rows were well separated: the value computed is 296 plot-units or 7.32 mlc. Only 6 other stands or types among 55 grasslands studied have with these two an Am value smaller than 2 mlc. The much smaller Am of G (.779 mlc.) than of F seems to be partly the result of a richer complement of species among the small annuals (16 in G, 12 in F, Daubenmire states). Higher density of individual plants may also contribute.

FESTUCA IDAHOENSIS–AGROPYRON SPICATUM ASSOCIATION, S.E. WASHINGTON. DAUBENMIRE (1942: 70-74). This more nearly mesophytic grassland has the spaces between dominant grasses occupied by large dicot herbs. Conspicuous among these are *Balsamorhiza sagittata, Lupinus, Potentilla, Sieversia, Geranium, Hieracium.* Species of high constancy include *Calochortus elegans, Clematis hirsutissima, Frasera albicaulis, Orthocarpus tenuifolius,* and *Zygadenus gramineus.* As in the preceding community, Daubenmire established 100 small plots in each of two undisturbed stands. These are in Whitman County, about 8 km. apart. One is just east of Pullman, and is shown in his Fig. 13. In each stand the frequency plots (Table 8) are 2 × 5 dm., arranged in 2 rows 1 meter apart, with 1 meter intervals between plots in a row. For this arrangement the estimated one-piece equivalent area is 5.93 mlc. (240 plot-units). Av. no. of spp. per small plot is 9.12 in stand A, 13.77 in B. Species in the 100-plot aggregate number 37 in stand A, 42 in B. Daubenmire gives additional data in each stand for areas of 1 to 10 sq. m. in a strip 1 meter wide, 10 meters long. His Table 7 shows for A, 22 spp. in the first 1-sq.-m. plot of the strip, 24 spp. in plots 1 and 2, 25 spp. in plots 1 to 6, etc. For the whole strip there are 29 spp. — The strip for stand B shows 24 in the first plot, 26 in 1 and 2, . . . to 31 spp. in the 10 plots. The compact area (no longer than wide) estimated to be equivalent to a 1 × 10 strip is 11.5 plot-units, with area in this case 2.84 mlc. For each stand two sets of points were thus available for plotting curves: 2

points from the group of 100 0.1-sq.-m. plots, 10 from the strip of 10 1-sq.-m. plots. Since the second set is not an average of replicated data, agreement is not very close. Daubenmire concluded that "the great bulk of the species in the stand is encountered in a single, random, meter-square plot. . . ." The species-area curves suggest that the number of species found in his first square meter ordinarily requires 2 sq. m. in Stand B, 8.5 sq. m. in A. The *average* square meter (as shown on the curve) has 20 spp. in B, 15.2 in A. An increase of area to 10 sq. m. brings no. of spp. to 34.8 in B, to 28.9 in A. It is interesting that the number of species Daubenmire observed in the first square meter is close to the Sr value determined by the curve (24 observed and 23.7 on the curve for B; 22 and 22.5 for A). The first 20 to 24 species encountered are sure to include many of the most important species of the community, so that Ar, the smallest representative area, is likely to satisfy some or most of the criteria which some students of vegetation might deem to be requirements for a minimal area. The area 5 Ar, or Am, thus seems to be a fairly conservative standard for minimum area.— Daubenmire noted (p. 72) that minimal area should be smaller in the *Agropyron–Poa* association than in the one dominated by *Festuca*.

DESERT GRASSLAND, SOUTHEASTERN ARIZONA

	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Grassland composite, Santa Rita Reserve	29.3	118.7	26.8	40.1	3

Desert grassland, south of Tucson, Arizona. D. Griffiths (1904). The map on p. 17 of this early study of sparse herbage in overgrazed range shows location of plots in a 49-square-mile tract within what was then the Santa Rita Forest Reserve. It is on the northwest foot-slopes of the Santa Rita Mountains. The present Range Reserve is larger than the early tract. The range was then overgrazed; after it was fenced, and cattle for a time excluded, the perennial grasses recovered rapidly. — As described in the bulletin, surface conditions and plant cover were extremely varied over the tract. Few perennials were encountered in the plots studied. The most frequent species listed, in descending order, are: *Lotus humistratus, Gilia floccosa, Plantago ignota, Eremocarya micrantha, Eriocarpum gracilis, Bouteloua bromoides, B. Havardii, Linanthus aureus, B. aristoides*. Moderately frequent species of *Aristida, Eriogonum, Astragalus, Eriophyllum,* and *Lupinus* are also present. — The plots were 7 × 3 ft. (0.4822 mlc.) 17 plots, A to Q, were recorded in spring, when winter annuals were evident; 11 plots, A′ to K′, in late summer. Selection of later plots was apparently unrelated to that of spring plots. Details are given on pp. 26-29. A few representative plot descriptions: C (n.w. part), "on a stony ridge in an area cut with steep, shallow ravines," (9 plants in 5 spp., dry weight 19 grains); E (w. part), "gently sloping grassy area at upper edge of heavier mesquite brush,"

(423 plants, 8 spp., 1710 grains); G (w. part of s. end), "old grassy area with mesquite" (883, 13, 2128); F′ (e. part of s. end), "Sandy alluvial bank about 8 ft. above shifting sands" (1182, 3, 2455). — To simplify the statistical treatment of these plot data, a table was made of occurrences of the 62 species in the 28 plots. Separate frequency percentages for spring and summer were computed. Average no. of spp. per spring plot, 6.88; per summer plot, 3.57. A method of combining spring and summer data indicated that if the same plots had been surveyed at both seasons the combined no. of spp. per plot would average 9.37. — For a species-area curve, aggregates from the 17 spring plots in 2-, 5-, and 12-plot units, as well as the average for 1 plot and the total for 17, were used. When plots are remotely scattered, the one-piece area equivalent to a plot-aggregate can be very large. Thus the one-piece area roughly estimated to include the 46 species recorded for the 17 separated plots is as big as 101 plots (52 mlc.). It is emphasized that the curve, and reference areas from it, apply to a composite of varied grasslands, not to a particular desert-grassland type. The 62 species encountered in Griffiths' 28 plots make a very small sample of the grassland part of the vegetational complex and of the rich grassland flora of the district studied.

Plot data giving actual counts are of value for many purposes; since those are less commonly provided in descriptions of grasslands, the details given by Griffiths will be especially useful. His numbers of individual plants per plot (21 sq. ft.), range from 4 to 8065. Entire count in 28 plots is 24,074. Mean density per plot is 860; per sq. ft., 40.94; per sq. m., 440.8; per milacre, 1783.

For herbaceous cover in creosote-bush desert of another Arizona district and of a California location, see p. 99.

GRASSLANDS IN EUROPE

Grasslands and other herbaceous types have been the earliest and the most frequent materials in plot studies of species and area. These studies were preceded by an interest in the general relation between extent of a natural geographic unit and the richness of its flora. Alphonse De Candolle's two-volume work on plant geography (1855, Chap. 7) expressed this relation clearly, and gave figures to illustrate it. Jaccard's early work (1902) advanced the knowledge of this relation, and Alvar Palmgren illustrated it in detail in his studies of the Åland archipelago (1917, 1922, 1925). Jaccard (1908, 1914) gave the subject a degree of precision by narrowing it to a specific study of measured areas within a stand of a particular, more or less homogeneous, community. It was considered interesting to make species-area curves from Jaccard's original plot data for subalpine grasslands in the Alps.

Du Rietz (1924: 31) states that the first grasp of the Minimiareal problem, i.e., of the fact that an association needs a certain area to give its most important species enough room, is found in Braun (1913) and Palmgren (1917).

Many of the central-European studies from about 1910 and thereafter con-

tain association-tables and other sets of data which should afford much material for species-area curves. Braun-Blanquet and others have studied minimal area from a point of view somewhat different from that of the present essay. Du Rietz and his associates in northern Europe emphasized the constant species (or what might be called first-order constants) in determining *Minimiareal.*

TABLE 16. Grasslands in Switzerland.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Subalpine prairies, Ormont: Area I	4.40	17.8	36.9	55.2	2
Area III	3.77	15.3	32.1	47.6	2
Area IV	3.86	15.6	29.4	42.9	2
Area VIII	1.74	7.42	22.9	33.7	2
Prairie near Chasseron, Jura Vaudois	9.21	37.3	45.0	66.4	1
Elynetum, central Alps (composite)	3.10	12.5	21.85	31.4	2
Caricetum mucronatae, n. Kalkalpen	0.48	1.94	19.1	27.8	3

SUBALPINE PRAIRIES, UPPER PART OF GRANDE-EAU VALLEY, COMMUNE D'ORMONT-DESSUS, ALPES VAUDOISES, 1050-1200 M. ELEV. PAUL JACCARD (1908). Nine groups of 1-sq.-m. plots, ca. 1 km. distant from one another, were situated "sur un terrain d'alluvion." Five are on slopes, four on level areas. 91 herb spp. were recorded on the 52 plots. The generally distributed species include *Trifolium pratense, Alchemilla pratensis, Chrysanthemum leucanthemum, Festuca pratensis, Dactylis glomerata, Leontodon hispidus, Campanula rhomboidalis, Trisetum flavescens, Anthoxanthum odoratum, Avena pubescens.* The 4 localities here treated, with species distinctive for each, are: I. S. slope at 1190 m.; *Plantago lanceolata, Carex sempervirens, Primula elatior.* III. N. slope at 1050 m.; *Deschampsia caespitosum, Knautia arvensis, Ranunculus montanus.* IV. W. slope at 1160 m.; exuberant prairie, fertilized; *Melandrium silvestre, Bromus erectus.* VIII. Prairie on level area; *Plantago media, Lotus corniculatus, Sanguisorba minor (dictyocarpa).*

A few of the statistics serving as the basis for the species-area curves are:

Locality	Species per plot		No. of Plot-sizes	Largest size, *mlc.*	No. of species
	Range	*Mean*			
I	22-35	28.25	8	1.98	53
III	25-31	27.13	8	1.98	45
IV	23-26	24.67	6	1.48	39
VIII	22-26	23.86	7	1.73	36

SUBALPINE PRAIRIE NEAR CHASSERON, JURA VAUDOIS. 1300-1350 M. ELEV. JACCARD (1914: 12). Jaccard recorded 25 1-sq.-m. plots in 2 up-slope rows on a mountain flank s. of Chasseron. He does not give a list of the species, of which there were 66 on the 25 sq. m. It was estimated that a compact plot of the same

area would have 61 species. Mean no. of spp. per 1-sq.-m. plot is 30. For 2, 3, 5, and 10 sq. m. the numbers are 34.8, 36.4, 39.0, and 45.0. On a later page he states that on 100 sq. m. the species number is 78; on 200 sq. m., 85. — The floristic mixture is richer and reference areas are larger than in any of the Grande-Eau localities.

Jaccard gives in the same article a detailed description of the *Pierrier de Sandalp,* which may perhaps be regarded as an inceptive grassland of stony alluvium. It and the sparse vegetation of his *Arête rocheuse de Sandgrat* were used for curves; the results are in a later group of communities of rocky surfaces.

Elynetum, 15 localities in central Alps. 2330-2750 m. elev. J. Braun-Blanquet (1932: 70-72). In a comprehensive association-table, details of area and of species number are given for this fine-textured alpine carpet dominated by the sedge *Elyna myosuroides.* Areas of 2 sizes are given for 10 of the locations. 13 locations are in East Grisons, 2 are in South Tirol. 11 species of lichens and mosses are omitted from the treatment, which consisted first in plotting on semi-logarithmic paper all points representing a species-number in a stated area. Points for the same location were joined by fine lines. From this array four points were estimated which represent a median trend through the swarm of given points. These are: 18.0 spp. at 1 sq. m., 24.4 at 4 sq. m., 34.3 at 20, and 38.1 at 40 sq. m. An S-curve through these four points is a composite curve for a generalized Elynetum. The width of the swarm in the first graph is such that reference areas for particular stands could be considerably larger or smaller than those determined for the composite curve. The minimum area from this curve is 3.10 mlc. or 12.5 sq. m. Braun-Blanquet does not mention his own value for minimal area of Elynetum, but indicates on p. 57 that it is larger than 4 sq. m. He states on p. 55 the minimal area for the mountain sedge meadow Curvuletum (10 sq. m.), and for the mountain bunch-grass Festucetum Halleri (20 to 25 sq. m.). — These minimal areas of Braun-Blanquet are in the same range of magnitudes as the Am-values for mountain grasslands in Table 16.

Caricetum mucronatae, n. Kalkalpen. H. Gilomen (1926). In this species-area study, Gilomen used plot-sizes 0.25, 1, 4, 16, and 64 sq. m. Details of species, and of numbers and arrangements of plots, are omitted from the condensed report. Data are included for one of the four communities studied. For this, the *Carex mucronata* association of calcareous sites in high mountains, species-numbers are 16.9, 24.8, 34.8, 36.4, and 37.8. These values were plotted directly. The S-curve of regular form which was tentatively drawn comes far from fitting the plotted points, but seems, until more data are available, as likely as any other. The resulting Am value, 0.48 mlc. or 1.942 sq. m., is the smallest found for any grassland.

TABLE 17. Grasslands: Denmark, Esthonia, Poland, Russia.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Maalǿv Krat, Denmark: 1-year Græsmark	1.87	7.55	21.7	31.4	3
8-year Græsmark	1.69	6.82	18.8	27.2	3
Markskellene	3.70	15.0	38.7	56.9	3
Festuca rubra on peat, Esthonia	4.70	19.0	21.4	31.8	2
Festuca rubra on loam, Esthonia	2.36	9.56	28.8	42.0	3
Prairie near Cracow: 1st example	1.63	6.56	21.9	31.8	2
2nd example	3.22	13.0	20.4	29.8	2
Steppe, District and Govt. Voronezh	15.1	61.1	57.8	83.7	3
Avena meadow steppe, Govt. Saratov	13.8	55.6	34.7	51.1	3

GRASSLANDS AT MAALǾV KRAT, DENMARK. RAUNKIAER (1910: 45-55, TABLE 10). These grasslands of formerly cultivated fields were sampled by Raunkiaer in the usual way, each with a series of 50 0.1-sq.-m. plots. For each series the effective plot-size is estimated at 0.2 sq. m.; the one-piece area equiv. to 50 plots is est. at 160 sq. m. or 35.54 mlc. The lists of spp. number 41, 47, and 78. The mean nos. of spp. per plot are 10.46, 9.78, and 12.26. The most frequent species in the 1-year græsmark are *Rumex acetosella, Lolium perenne, Anthemis arvensis, Poa annua, Alchemilla arvensis, Scleranthus annuus.* In the 8-year grassland: *Achillea millefolium, Ranunculus repens, Festuca rubra, Poa pratensis, Agrostis vulgaris.* In the Markskellene: *Festuca, Agrostis, Achillea, Galium verum, Campanula rotundifolia.*

FESTUCA RUBRA MEADOW, SAGNITZ, ESTHONIA. K. REGEL (1921). On two areas Regel established 0.25-sq.-m. quadrats, clipped and dried the herbage, separated it by species, and weighed it. His maps (Figs. 1 and 2) and tables (4 to 6) show arrangements of plots, and dry weight for each species on each plot. Two features are notable: the relatively fine texture in comparison with most other grasslands; and the considerable variability of composition from spot to spot. Regel rightly considers it a complex of many different components: he calls them associations. Most grasslands similarly are mosaics of unlike elements; to the extent that the same combination of elements is repeated over a sizable area, such a mosaic has its own degree of uniformity, and thus qualifies as an association in the American use of the term, though in fact it is an association-complex. One stand reported is on dry peat, the other on loamy soil. The two show marked difference in floristic richness, with 11.54 and 18.45 species per plot. In the stand on peat, *Festuca rubra* is strongly dominant with 62% of the total herbage. The other important species are *Salix rosmarinifolia* with 8.7%, *Stellaria glauca, Rumex acetosa, Carex vulgaris, Comarum palustre, Betula pumila, Agrostis stolonifera* 1.9%. The other area with loamy soil has only 16.5% of *Festuca rubra;* other leading species are *Phleum pratense* with 11.9%, *Poa trivialis, Poa pratensis* 8.8%, *Deschampsia caespitosa, Festuca pratensis* 5.9%, *Carex panicea* 5.0%.

Plots are systematically located: 13 in a large square in the peat area (with 1 additional larger plot), and 20 in a large rectangle in the loamy area. Regel assigns each plot to its type according to composition. Differences of composition greatly restrict the grouping of plots into aggregates for species-area treatment; only those of the same type (or of not too unlike composition) were grouped together. The ratio in an aggregate of its mean number of species per plot to the general average number per plot was applied as a correction to the apparent number of species in the aggregate. The following array shows the species-area basis for curves.

Unit or aggr., sq.m.	0.25	0.5	0.75	1.0	4.0	5.0
Equiv. 1-piece area, mlc.	0.062	0.40	.76	1.11	4.12	5.92
Spp.-no., peat	11.54	15.4	19.6	22.6	31	—
Spp.-no., loam	18.45	27	30.3	35.8	—	51

The curve for the peat area fitted the plotted points very well, the curve for the loam area only passably. For this reason the dependability-rating for loam-area results is 3 instead of 2.

Prairies near Cracow, Poland. E. Malinowski (1911: 331-335). Using methods of Jaccard, Malinowski gave details for two areas of natural grassland, with 7 1-sq.-m. quadrats in each. Species occurring in all plots in the first area are: *Convolvulus arvensis, Euphorbia* sp., *Festuca elatior, Fragaria collina, Helianthemum vulgare, Medicago* sp., *Salvia pratensis, Silene nutans.* In all plots of the second example: *Equisetum* sp., *Galium Mollugo, Mentha* sp., *Poa pratensis, Ranunculus repens.* Spp. per plot: 21.4 and 15.7. In all 7 plots: 32 and 28 spp. For each example, species-numbers were also found for aggregates of 2, 3, 4, and 5 plots.

Steppe, District and Government Voronezh. Boris A. Keller (1927: 218-220). In two 100-sq.-m. areas of steppe on deep-soiled chernozem, Keller recorded 96 and 86 species. A supplementary list gives 32 additional species found in the same steppe outside the two areas. Observations were made in June, 1926. The abundant species: *Festuca sulcata, Bromus erectus, Poa pratensis* var. *angustifolia, Koeleria gracilis, Phleum Boehmeri, Carex praecox; Draba repens, Thymus Marschallianus, Filipendula hexapetala, Taraxacum vulgare, Potentilla opaciformis.* — A species-area curve was drawn, using for 100 sq. m. the mean species-number 91, and for 1 sq. m. a roughly estimated 19 spp.

Avena desertorum meadow steppe, District of Kuznétzsk, Government Saratov. Keller (1927:220). Abundant species: *Avena desertorum, Phleum Boehmeri, Festuca sulcata, Stipa dasyphylla, S. joannis; Anemone patens, Artemisia sericea, Filipendula hexapetala, Trifolium montanum, Achillea setacea, Inula hirta,* and *Veronica spicata.* This meadow steppe was studied in August, 1905. Keller listed 68 spp. in 460 sq. m. The est. no. of spp. at 1 sq. m. is 12.

TROPICAL SECONDARY GRASSLAND

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Cogonal, Luzon	3.58	14.5	17.6	25.1	3

Cogonal, base of Mt. Maquiling, Luzon. Brown and Mathews (1914: 461). In spite of strong dominance of the tall cogon grass, *Imperata exaltata,* with 1 to 6 stalks per plant and 1976 plants in the 4-sq.-m. plot recorded, many herbs and small shrubs and vines are also present. Of these, one should mention *Desmodium pulchellum, Mimosa pudica, Selaginella Belangeri, Synedrella nodiflora, Ipomoea triloba, Merremia hastata,* and *M. umbellata. Riccia* plants are numerous. Since counts of individuals are given, it is possible to approximate the figures for smaller plot-sizes, estimating for each species the number of plots of a given size in which it will occur, from available number of plants per plot.

(The method is an outgrowth of a plot-map analysis of Brownfield Woods. From the figures obtained, graphs were made for a number of tree species over a wide range of plot-sizes, correlating the proportion of plots containing the species with the number of individuals available per plot. With the same number of plants available, proportion of plots in which the species occurs is independent of size of plot. A table prepared from the graphs gives approximate frequency of occurrence in plots for any species not showing strong tendency toward aggregation.)

Before applying this method to the cogonal, each number given for seedlings of a species was scaled down and added to those of larger plants; the number given for *"Compositae"* was apportioned among a presumed 4 different species, and *Riccia* was excluded from the list. In the detailed table made for 4 plot-sizes, there were 1976 + 329 individual plants of 19 spp. in the 4 sq. m.; 52.2 occurrences in 4 plots of the 1-sq.-m. size: thus 13.05 spp.; there were 123.9 occurrences in 16 0.25-sq.-m. plots of 7.74 spp.; and 251.3 occurrences in 64 0.0625-sq.-m. plots of 3.93 spp. — These species-numbers for the 4 sizes determined the lower part of an S-curve of rather feeble curvature, with point of flexure suggested slightly above the 4-sq.-m. plot size.

GROUND COVER OF FORESTS

There are many forms of transition between grasslands of open habitat and field-layer vegetation in shade under tree canopy. In forest ground-covers which have been studied, reference areas are considerably larger than in most grasslands. This may be a consequence of the broader leaves and more diffuse growth-form of most shade-plants, in contrast to the linear or much-divided or reduced leaves of grasses and dicot herbs of the open, with usually extreme crowding of plant individuals. Because of its transitional character, and of its importance in

the development of species-area studies, Gleason's vegetation of the open parts of burnt-over pine lands in Michigan is first examined. Since the large-toothed aspen, *Populus grandidentata,* is the common tree in the sandy soils of these former pine forests, such tracts are spoken of as the aspen association or "the aspens," but the open parts are treeless over various-sized areas up to several acres. Aspens may be thinly scattered in these open parts; in other places small groups or fair-sized groves or stands of aspens occur, usually with some other tree species which soon follow. Thus there are two kinds of vegetation, actual young forest, and a herb–dwarf-shrub ground cover which has elements of grassland, of dwarf shrub, and of open-forest undergrowth. Probably only young forest should be called "aspen association." It is the herb–dwarf-shrub cover, dominated in most parts by *Vaccinium pennsylvanicum* and *Pteridium aquilinum,* in which Gleason's studies were made. The first data were published in 1920, species-area results from the same data in 1922, and additional results from new data in 1925.

TABLE 18. Bracken—Blueberry Ground-Cover, Michigan.

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Area of earlier study (1922)	57.5	232.5	17.7	26.6	1
Series 1, Tract 1 (1925)	47.7	193.0	20.3	30.3	3
Tract 2	49.6	200.6	21.2	31.6	3
Series 2, Tract 4	62.4	252.1	35.4	50.6	3
Tract 5	59.4	236.1	27.6	39.7	3
Tract 6	49.0	198.1	33.0	47.4	3
Tract 7	67.2	271.3	32.0	46.0	3
Tract 8	73.7	298.0	34.8	49.6	3

BRACKEN–BLUEBERRY GROUND-COVER AMONG ASPENS, NORTHERN LOWER MICHIGAN. H. A. GLEASON (1920, 1922, 1925). Most of Gleason's studies were made near Douglas Lake, not far from the north end of the lower peninsula. Each tract consists of a considerable number of 1-sq.-m. quadrats. The 1920-22 data cover 240 such plots, with 27 spp. Mean no. of spp. per plot is 4.375. Each of these species-numbers is for a single compact area. For intermediate plot-sizes: 4-sq.-m. plot-groups average 7.60 spp.; 16-sq.-m. size, 12.0 spp.; 60-sq.-m. size, 19.75 spp. These intermediate-sized areas are contiguous quadrats in a row, and are less compact in form as the number of quadrats increases.

Gleason's species-area graph had a rather small vertical scale for number of species, and its configuration of points shows rather small departures from those which a straight line would fit. This is the earliest graph known to the writer in which mean number of species is plotted against logarithm of area. (O. Arrhenius had developed a formula, published in 1920, for which the graphic analogue is a plotting of logarithm of species-number against logarithm of area. Du Rietz's "Methodologische Grundlage" includes graphs so constructed for seven communities in Sweden [1921: Figs. 18, 19; pp. 205-206]. These graphs

show lack of agreement with Arrhenius' formula. Du Rietz put greater stress on his other graphs showing number of *constant* species plotted against area, and against log area, as well as log number of constants plotted against log area.) Gleason inferred from his graph that species-number is directly proportional to logarithm of area. Later he came to realize that the relation is not so simple as to be represented by a straight-line graph.

It is of interest, in view of the much later finding that the usual species-area graph on semilog paper is S-shaped, to reexamine the graph published by

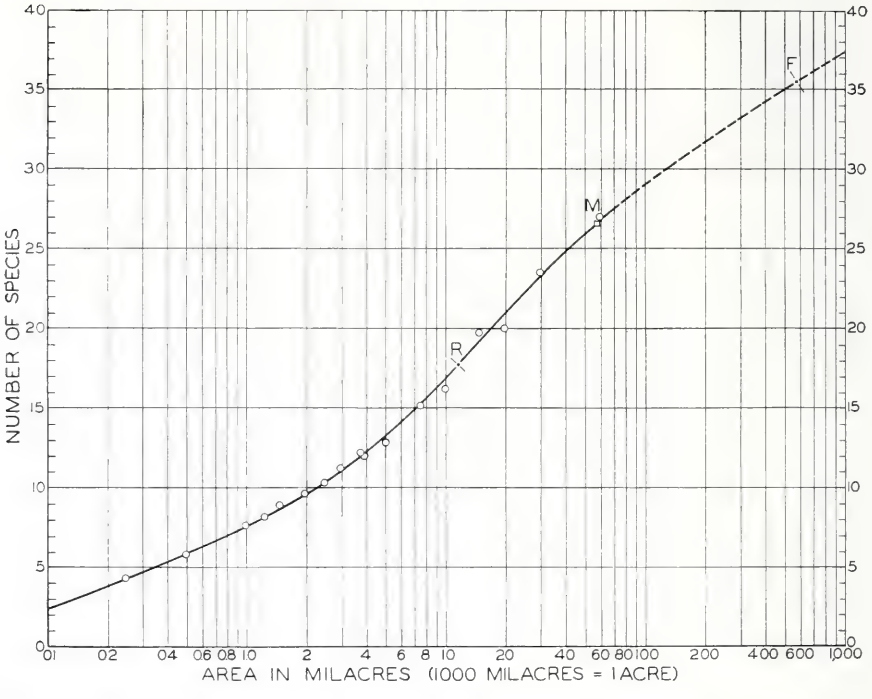

FIGURE 4. Gleason's species-area graph of 1922 for bracken–blueberry ground-cover in Michigan, redrawn as a smoothed S-curve. The original was the first graph of this type, so far as the writer is aware. Minimum area is 57.5 milacres, with 26.6 species. This growth of herbs and low woody plants covers the mostly treeless parts of sandy aspen lands.

Gleason in 1922 (his p. 161). The *S* form is evident, the lower part of the curve being concave, the upper part slightly convex. Gleason's figure is thus the first graph of the type adopted in this study 22 years later. When Gleason's graph is redrawn as a smoothed *S*-curve (Figure 4), it is seen that the fit is good.

In Gleason's publication of 1925, figures are given for 7 additional locations in the aspens, in two series, Tracts 1-2 and Tracts 4-8. Although an adequate number of points was available for the 1922 curve, plot-sizes for some tracts in the 1925 article were few, and the sizes intermediate between smallest and

largest were aggregates of well-scattered plots, rather than single compact areas. An adjustment comparable to an I-conversion, to find numbers of species in a one-piece area of the same total extent, was therefore necessary.

Tracts 1 and 2 had 3 intermediate sizes: 4, 16, and 64 sq. m., while Tracts 4 to 8 had only one: 100 sq. m. Curves for Tracts 1 and 2 were made by plotting the given points on the same sheet as the 1922 curve, and patterning the form of the new curves after that of the old one. For the others, the S-curve for Tract 1 was compared with a graph made to fit the non-adjusted Tract-1 values. From this graph, the species-number for 100 scattered quadrats was found to be 27.46; from the S-curve the approximate value for a 100-sq.-m. compact area was found to be 26.43. The rather slight reduction in number of species at this plot-size was the chief means of estimating the adjusted *S*-values for Tracts 4 to 8. The whole array of given values and adjusted values may be seen in the accompanying table, in which *A* represents area in square meters, *S* represents number of species. For Tracts 1 and 2, those *S*-values which were read from the graphs are shown in parentheses.

TABLE 18a. Species-Area Data for Bracken—Blueberry.

Tract	*S* at 1 sq. m.	Intermediate areas: *A*	Given *S*	Adjusted *S*	Largest area: *A*	*S*
1	4.82	16	17.38	(14.82)	256	32
		64	25	(23.72)		
		100	(27.46)	(26.43)		
2	4.88	16	19.0	(15.07)	256	33
		64	28.0	(24.31)		
4	4.19	100	44	41.85	8492	84
5	4.62	100	34	33.0	4350	59
6	4.75	100	44	41.5	8895	77
7	4.15	100	39	37.5	6142	70
8	4.15	100	41	39.5	44331	91

HERBACEOUS GROUND COVER UNDER FOREST

The first group of these herbaceous ground-cover communities under fairly dense tree canopies comprises four forests in Michigan of aspen-birch and beech-maple types (Table 19). It is presumed that tree seedlings are included in the counts for some of these and of other forest field layers. Also in Table 19 are beech forests and oak forests in Europe. Two very different types are appended: herbaceous field layer under spruce in Denmark, and a relict sand-prairie vegetation under more or less open blackjack oak in the Illinois River dunes.

TABLE 19. Herbaceous Ground-Cover under Forest.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Aspen–birch, Michigan: Tract 3	73.8	298.3	21.2	31.7	3
Beech–maple, Emmet Co.: Tract 9	68.4	276.8	14.9	22.1	3
Beech–maple, Antrim Co.: Tract 10	65.8	266.2	23.1	34.4	3
Beech–maple, s.w. Michigan	75.8	306.9	21.5	31.7	3+

TABLE 19 (*continued*). Herbaceous Ground-Cover under Forest.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Beech, Gribskov	79.3	320.5	17.0	24.7	3
Beech, Farum Lillevang	48.8	197.7	19.2	28.4	3
Beech, Jonstrup Vang	116	469.2	12.1	17.9	3
Oak, Jonstrup Vang	43.1	174.4	29.8	43.4	3
Spruce, Egebjergene	81.7	330.8	14.3	20.9	3
Quercus marilandica, Illinois	163	660.0	16.0	24.0	2

GROUND-COVER UNDER ASPEN AND BIRCH, MICHIGAN. GLEASON (1925:67). This was studied "in a dense grove of *Populus* and *Betula,* with the ground heavily shaded and with some accumulation of leaf mold." It contrasts with bracken–blueberry cover of open areas within the aspen lands already described. This shaded undergrowth is listed as Tract 3 of Series 1, and like Tracts 1 and 2, comprises 256 1-sq.-m. quadrats, with species-numbers for 1, 4, 16, 64, and 256 plots: intermediate sizes are aggregates of scattered plots. Spp. per plot, 3.06; in 256 plots, 31. For the 64-plot aggregate, 22.75 spp. Reduced species-number for compact single area of 64 sq. m., 21.3.

GROUND-COVER UNDER BEECH–MAPLE FORESTS, MICHIGAN. SERIES 2, TRACTS 9 AND 10. GLEASON (1925). Tract 9 comprises 2500 sq. m. in a 40-acre stand in Emmet Co. Tract 10 covers 6400 sq. m. in a remnant of 100 sq. miles of forest in Antrim Co. They were recorded in the same manner as bracken–blueberry Tracts 4 to 8, and curves were made from the data as for Tracts 4 to 8. The species-numbers are:

Tract	For 1 sq. m.	For 100 scattered plots	For 1 plot of 100 sq. m.	For whole tract
9	2.93	19	17.65	32
10	3.73	30	28	46

GROUND-COVER UNDER BEECH–MAPLE FOREST, SOUTHWESTERN MICHIGAN. L. F. KENOYER (1927:344). The extremely condensed data give the number of species in each of 5 frequency classes (20% steps), in 25 quadrats, each of 10 sq. m. From these figures a distribution was made, showing the likely number of plots in which each of the 37 species occurs. Thus for the highest class, 81 to 100%, 1 of the 2 species was assumed to occur in 25 plots, the other in 23. The total number of occurrences per plot was estimated to be 202, making 8.08 species per plot. This may be somewhat too high. Since the plots were separated, fewer than 37 species would occur in a compact 250 sq. m. plot. The reduced number for this size was estimated at 30.5. Such a curve, based on two points, is of only suggestive value; it gives reference areas somewhat larger than those for Gleason's three stands. Superposed on the graph for these forests, it nearly coincides with the curve for Tract 3, aspen–birch, but has slightly steeper gradient.

GROUND-COVER UNDER BEECH FOREST, GRIBSKOV, DENMARK. 4 LOCATIONS. M. VAHL (1911: 334, TABLE 2). The table summarizes occurrence in 50 0.1 sq. m. plots of 5 woody and 35 herbaceous species in each of 7 stations, 5 being in the forest known as Gribskov, or Grib Skov, not far from Copenhagen. Omitting station D (less rich in species), and eliminating tree and shrub species, the following data apply to the four Gribskov stations A, B, C, and G, in order. Spp. per plot: 4.7, 4.48, 6.06, 4.78. Spp. in 50 plots: 12, 14, 17, 14. In the 4 series of plots: 34 spp. For the composite of four series: 5.01 spp. per plot, 14.25 spp. in 50 plots. Estimate of effective plot-size, 0.3 sq. m. One-piece area equiv. to 50 scattered plots: 28.8 to 48 sq. m. One-piece area large enough to include 34 spp., 2400 to 4500 sq. m. Minimum areas for similar stations would presumably range from 60 to 100 milacres. One reason for their considerable extent is that much of the area is occupied by tree seedlings, saplings, or shrubs. Also, as in many other forests, heavily shaded parts may have only a few individuals of the few species that can endure both heavy shade and the smothering effect of repeated falls of dead leaves from the tree-crowns above. — In Gribskov, *Fraxinus excelsior* is a moderately frequent companion of *Fagus silvatica*. Herbs of high frequency in at least two of the four stations are *Anemone nemorosa, Asperula odorata, Oxalis acetosella, Mercurialis perennis* and *Milium effusum*. Frequent in individual stations are *Equisetum silvaticum* in A; *Maianthemum, Convallaria, Trientalis,* and *Poa nemoralis* in B; *Stellaria holostea* and *Viola silvatica* in C; and no distinctive species in G.

BEECH UNDERGROWTH, FARUM LILLEVANG, AND JONSTRUP VANG (NOT FAR FROM COPENHAGEN). RAUNKIAER (1910: 60-64). These are 2 of 7 beech ground-covers summarized in Raunkiaer's Table 15. Herbs only are included in these series of 50 0.1-sq.-m. plots. Spp. per plot and spp. in 50 plots for these 7 stations are: No. 1, Jonstrup Vang, 1.60 and 12; 2. Nørreskov, 3.4 and 15; 3. Lille Hareskov, 3.08 and 8; 4. Vallø skov I, 3.8 and 10; 5. Vall skov II, 4.4 and 12; 6. Farum Lillevang (the richest in spp.), 6.22 and 20; 7. Bognæs (the poorest), 1.22 and 6. In the last, *Allium ursinum* is dominant. At Farum Lillevang, *Anemone nemorosa, Milium effusum, Oxalis, Asperula, Viola silvatica* and *Melica uniflora* occur in 50 to 29 plots. At Jonstrup Vang, only *A. nemorosa* is dominant (in 50 plots). *Oxalis* is in 8 plots, *Melica* in 3. In a more detailed table for the *Anemone nemorosa* facies on p. 29, Raunkiaer lists in 100 0.1-sq.-m. plots, only 7 spp. which occur in more than 1 plot. Aside from the dominant *Anemone, Gagea lutea* is in 17 plots, *Oxalis* in 16. Plot-numbers for the next 4 spp. are 5, 4, 3, and 2. — The curve for Lillevang was made in the manner described for Vahl's Gribskov ground-cover. For Jonstrup Vang the detailed table gave independent data for 4 plot-sizes: 0.01, 0.1, 1.0, and 10 sq. m. The species-area curve gave the Am-value of 116 mlc. This large minimum area is attributed to the pronounced dominance of *Anemone,* which leaves so little room for other herbs that a large surface must be surveyed.

Oak undergrowth, Jonstrup Vang. Raunkiaer (1910: 57-60). 4 locations near Jonstrup Vang are given in 4 columns of Raunkiaer's Table 13. Number 4, considered most nearly representative, is west of the place known as Maalø̈vmose. The herb cover is named *Convallaria majalis–Aira flexuosa* facies. The most frequent plants are *Convallaria, Aira, Anemone, Maianthemum,* and *Viola silvatica.* There are 34 spp. in the 50 0.1-sq.-m. plots. Spp. per plot, 6.04. Estimated one-piece area equivalent to 50 plots, 34.6 sq. m., = 14 mlc. If curve and computations are approximately correct, this herb cover under oak has smaller reference areas (Am is 43.1 mlc.) than any of the 16 other forest undergrowths of Tables 19 and 20.

Oxalis acetosella facies under Picea excelsa, Egebjergene, near Jonstrup Vang. Raunkiaer (1910: 70-75). In four 50-plot series, Raunkiaer gives data for *Aira flexuosa* facies with 8 spp., *Aira–Oxalis* facies with 9 spp., and two examples of *Oxalis* facies, with 6 and 10 spp. The last was made the basis of a curve. The location is in a *Granskov* near a beech forest bordering its southern part. Spp. per plot, 1.34. Estimate of one-piece area including 10 spp., 15 sq. m. or 6.18 mlc.

Sand-prairie ground-cover under blackjack oak, Illinois River dunes. Gleason (1907: 175, Table 10). Most stands of the xeric *Quercus marilandica* are young, the shade and leaf-litter are not heavy and the sand-prairie vegetation present before invasion of the trees is still the only ground-cover. The same is true of young stands of black oak, *Q. velutina,* in the dunes. There is also an older dune forest of mixed composition in the river dunes adjoining the east bluff of the Illinois River, with true forest-herb undergrowth, but an almost complete change of ground flora takes place in its development. In the xeric young forest away from the river, the ground flora is practically identical with that of treeless areas, with higher frequency and greater abundance of a few species, notably *Tephrosia virginiana,* a legume with handsome pea flowers, and the poppy mallow, *Callirrhoë triangulata.* Gleason's strip of 17 plots, each 10 × 10 ft., does not include *Callirrhoë.* 12 plots are in a brushy part of a blackjack stand, 5 are in a more open part. Since the most frequent species are the same in both parts, they are here treated as a unit. These most frequent species are: *Tephrosia, Opuntia humifusa, Aristida tuberculosa, Euphorbia corollata, Teucrium canadense,* and a bushy shrub, the sand form of *Rhus aromatica.* This last is not part of the herb cover, but is everywhere at home in sand prairie, as thinly scattered bushes, or forming clumps or extensive low shrubberies. (It is an effective sand-binder and dune-former: an important component in the vegetation complex of the dunes.) — Gleason's 17 plots include 18 spp. Spp. per plot, 5.88. Recombinations of plots gave data for 5 intermediate plot-sizes. The compact area equivalent to the 17-plot strip is est. at 46.8 milacres. Reference areas are larger than for true forest ground-covers, or for sand prairie. *Tephrosia* and *Rhus* occupy much space; most other species are thinly scattered.

DWARF-SHRUB GROUND COVER OF BOREAL FORESTS

North European plant geographers have recorded many examples of field-layer vegetation under trees or in the open parts of scattered-tree stands. Birch, Scots pine, spruce, and juniper are the common tree species. Dwarf shrubs are the usual dominants. With them are seedlings and stunted individuals of the trees, herbs of many types, including *Lycopodium* and true-fern species, grasses, sedges, and wood-rushes. Mosses and lichens, though frequently listed or mentioned, are not included in the present counts. The tall-shrub and tree species when listed are taken to be part of the field layer, and are included in the counts. It is not usual to find an explicit statement whether small plants of these larger species are or are not part of the field layer.

TABLE 20. Boreal Dwarf-Shrub Ground Cover Under or Among Trees.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Vaccinium—birch, Island Jungfrun	59.3	240.0	12.6	18.6	3
V. vitis-idaea—pine, Järvis, Finland	57.6	233.1	17.4	25.2	3
V. vitis-idaea—pine, Hillilä, Finland	62.2	251.4	18.9	27.5	3
Vaccinium—pine, Järvis, Finland	66.5	269.0	21.5	32.0	3
V. myrtillus—pine, Kola peninsula	107.0	433.1	12.3	18.3	3
V. myrtillus—pine, Island Sandön	95.2	385.0	13.1	19.5	3
Same, pines excluded from count	110.5	446.8	12.8	19.0	3
Calluna—pine, Island Sandön	49.0	198.3	5.64	8.16	3

VACCINIUM AND OTHER DWARF-SHRUBS UNDER BIRCH, ISLAND JUNGFRUN. DU RIETZ (1921: 148). (NACKTER PREISELBEERBIRKENWALD.) Jungfrun is about 20 km. east of the mainland of southern Sweden in lat. 57° 15′; it is in the northern opening of Kalmar Sound, about 8 km. west of the long island Öland. Du Rietz specifically lists each larger species in each of the layers in which it occurs. *Betula alba, Juniperus communis, Q. robur, Rhamnus frangula,* and *Sorbus aucuparia* are in the field layer. *V. vitis-idaea* is dominant, though *V. myrtillus* is likewise present in all plots recorded (44 of 1 sq. m., 10 of 4 sq. m.). *Calluna* and *Empetrum; Melampyrum, Deschampsia flexuosa,* and *Pteridium,* are notable. Mosses and lichens are infrequent. — Effective small-plot size is 0.3 mlc., with 5.38 spp.; for the larger plots 1.06 mlc. with 7.9 spp.; 15 spp. in 21.1 mlc.

VACCINIUM VITIS-IDEA–PINE, JÄRVIS IN PARISH OF NASTOLA, FINLAND. K. LINKOLA (1922: 16-21). Linkola studied in July, 1917, 7 stands of *Vaccinium* under pine. This locality, no. 4, is a moderately steep north slope with 50-year pines. The plot, taken to be 15 meters square (55.6 mlc.), has 2 conifers, 2 dicot tree spp., 2 dwarf shrubs (no *V. myrtillus*), 15 dicot herbs, 5 grasslike herbs, 3 other monocot herbs, 3 mosses, 1 lichen. At least 25 spp. are in the field layer. Curves for this and 2 others of Linkola's stands were made possible by the presumed similarity in form to the curve for Du Rietz's Heidelbeerkiefernwald.

V. VITIS-IDAEA–PINE, No. 6, HILLILÄ IN ASIKKALA PARISH. LINKOLA (1922). A few plants of *V. myrtillus* are in the no. 6 plot, which has 25- to 75-year-old pines, and is at the foot of a ridge. It is somewhat richer in composition, with 4 dwarf-shrub spp. and *Pteridium*. At least 27 field-layer spp. are in the plot.

VACCINIUM–PINE, No. 3, JÄRVIS. LINKOLA (1922). On flat top of a ridge (Åshügel). 10- to 70-year-old pines. 3 dwarf-shrubs, 20 dicot herb spp., 6 grasslike herbs, no lichens. *V. myrtillus* and *V. vitis-idaea* equally abundant. 37 spp. in all, at least 31 in the field-layer on the plot.

V. MYRTILLUS–PINE, KOLA PENINSULA. K. REGEL (1923: 65). (Aufnahme No. 20, in Pinetum myrtillosum, July, 1913). Plot is 10 × 10 steps, taken to approximate 9 × 9 meters (870 sq. ft., or 19.93 mlc.). *Pinus lapponica* and *Picea excelsa; V. myrtillus, V. vitis-idaea, Empetrum, Calluna, Ledum palustre.* Several herb spp., including *Lycopodium annotinum*. No grasses; 2 moss spp. Including the 2 trees, 12 spp. are in field layer of the plot. Curve is patterned after that of Du Rietz, which follows.

V. MYRTILLUS–PINE, ISLAND SANDÖN. DU RIETZ (1921: 149-153). (MOOSREICHER HEIDELBEERKIEFERNWALD.) Sandön is in the Stockholm Skärgård close to the east-Swedish coast. It is about 35 km. east of Stockholm. The only tree is *P. silvestris*. The 5 dwarf-shrubs are *Vaccinium* (2 spp.), *Calluna, Empetrum, Arctostaphylos uva-ursi*. As in the case of one or two dwarf-shrub heaths, (treated in an earlier section), Du Rietz presents a detailed summary for 6 plot-sizes; 1000 plots of 0.01 sq. m., 250 of .04, 40 of the .25-size, 330 quadrats of 1 sq. m.; 80 of 4 sq. m., and 20 of 16 sq. m. Effective plot-sizes and one-piece areas equivalent to the different aggregates were estimated. Species-numbers ranged from 2.67 at the effective size of .03 mlc. to 20 at 127.7 mlc. These numbers include the pine. A curve was drawn for this array, and a second curve for the same plot-sizes omitting the pine. The difference in results may be seen in Table 20. When the tree species is excluded, considerably larger reference areas are required.

CALLUNA–PINE, SANDÖN. DU RIETZ (1921: 153). (FLECHTENREICHER CALLUNAKIEFERNWALD). This combination is extensive on sandy soils in various parts of Sweden, and elsewhere. *Calluna* and *V. vitis-idaea* are the chief constants, with *P. silvestris. Arctostaphylos, V. myrtillus,* and *Empetrum* are the other dwarf-shrubs. *Melampyrum* and *Festuca ovina* are present. *Cladonia rangiferina* covers much of the ground surface. Although Du Rietz does not list small pines as part of the field layer, trees are indicated as present in or covering all of the 4-sq.-m. and 16-sq.-m. plots. Arbitrarily estimated frequencies for the 4 smaller plot-sizes have been added to his table in order to compute species-numbers. Only 8 spp., including pine but no lichens or mosses, are given in the table. Species-numbers range from 1.62 for the .01-sq.-m. size (effective area .03 mlc.) to 8 spp. at an estimated 44.2 mlc. This heath-forest ground-cover

has smaller reference areas than any others composed chiefly of dwarf-shrubs. There is more reason to exclude pine from the count for this heath forest than from the *V. myrtillus* ground-cover. If this were done, the reference areas would probably still be no larger than in any of the other dwarf-shrub covers.

The reader may find some interest in comparing these field-layer communities under or among trees with their equivalents in treeless areas, as previously included in Table 10 (heath and dwarf-shrub): Am-values 21.3 to 61.7 (two extreme types omitted). The generally larger reference areas in forested country are expectable: tree-trunks, dense groups of young conifers, heavily-shaded spots, etc., make numerous breaks in the field layer. — Certain similarities to the bracken–blueberry ground-cover in Michigan could be suggested. Ranges of minimum areas are: 47.7 to 73.7 mlc. for bracken–blueberry; 49 to 110.5 mlc. for the more diverse European types of Table 20. Species-numbers are generally higher in bracken–blueberry.

One more forest ground-cover study must be reported. T. A. Noskova published in 1928 an article in Russian on minimal area in forest associations. The original has not been seen, but the summary by G. A. Lebedeff in Biological Abstracts (Entry 21350 in Volume 6) is useful. Minimal area is defined as the smallest plot of land on which all of the peculiarities of a given plant association are developed. For three types of forest the minimal area was found to be 500 sq. m. (123.6 mlc.). These types are Pinus–Pteridium–Hylocomium, Pinus–Quercus–Tilia, and Pinus–Quercus–Pteridium. For the Pinus–Cladina type it is 400 sq. m. (98.8 mlc.). If, as is likely, the tree species in any one stand are few, the minimum area for trees may be no larger than that given for plants of the ground layer. The minimal areas given for these Russian forests are in a size range which overlaps the larger Am values for the northwest-European forests in Table 20.

GROUND VEGETATION WITHIN TROPICAL FORESTS

The only examples used for ground-cover in tropical forests are those of J. G. B. Beumée (1922) for stands of teak (*Tectona*) in Java. The original publication was not available; data were taken from the compact summary by O. Arrhenius (1923: 69, Table 3). This does not include descriptions, but considerable information is provided in Markgraf's abstract.

Table 21. Herb and Lower Woody Vegetation, Teak Forests, Java.

Stand	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Beumée's No. 16a	910	3677	41.1	61.9	2
23b	797	3223	13.8	20.9	3
23a	712	2878	14.8	22.3	3
26	705	2851	50.8	76.0	2
21a	680	2751	32.1	47.3	3
33	660	2667	42.3	61.6	3
18	484	1959	75.3	111.1	2

Ground or lowest-story vegetation in teak forests, Java. Beumée (1922). It seems likely from descriptions of other tropical forests that the undergrowth is very different from that of most temperate forests. There are fewer and much larger herbs, few or no rounded or flat-topped shrubs, but in their place, crowds of slender arbuscules of many species and of varying height. Large-tree species are usually represented by varying numbers of seedlings and young trees. There may also be course grasses, especially in disturbed areas. Understories in Beumée's stands evidently differ widely, in floristic richness and in rate of increase of species with area, as shown by greatly differing steepness of the curves. The number of given plot-sizes varies from 4 to 7. Largest plot-size (with 39 spp.), is 1400 sq. m. (locality 21a). For 3 other stands the largest plot-size is 1200 sq. m., with 49.5 to 103.7 spp. Smallest plot-size is in all 7 instances 100 sq. m., with species-numbers from 4.5 in No. 23b to 40 in No. 18. No. 23b has only 16.7 spp. at the largest size given, 1000 sq. m. The steepest curve, that of No. 18, suggests that a high rate of species-increase continues into much larger areas than in temperate forests: i.e., the supply of additional species available within the district and able to enter into the mixture is perhaps 5 to 10 times as great as in a floristically rich temperate-forest district. Because of this continued rate of species-increase (and of the greater size of the plants), reference areas of No. 18 are larger than in ground-covers of any temperate-forest examples studied. The largest Am value in Tables 18-20 is 116 mlc. (if we exclude the somewhat aberrant ground vegetation under blackjack oak, 163 mlc.). This compares with 484 mlc. for teak stand No. 18.

The other teak stands have even larger reference areas, but not as the probable consequence of their having many species, nor from persistent rate of species-increase. More information is required for these stands. It may be added that the Am values in Table 21 are conservative, and that fuller information might give considerably larger areas. For example, if the S-curve for No. 18 is made to fit the points exactly (it is possible in this case), the resulting Am is 662 mlc., with correlated Sm of 121 species.

Markgraf notes: "Wenn man nun feststellt, wieviel Prozent aller Arten den Probequadraten eines Bestandes gemeinsam sind (nach Jaccard), so erhält man erst für die 4000-qm-Flächen einen Wert, der dem von Jaccard für 1-qm-Flächen in europäischen Wiesen gefundenen nahekommt. . . ."

BOG VEGETATION

Results for nine sets of data on bog communities are shown in Table 22. Four of them are dominated by dwarf-shrubs; in the second group of four, sedges are dominant, although *Vaccinium oxycoccus* (cranberry) is abundant in some of them. The ninth enumeration includes only bryophytes. These nine examples are treated as one-layered communities; differentiated results for field and moss layers are given, in a later section on vegetation of mixed growth-forms, for some three-layered raised-bog communities described by N. and S. Katz (1926).

TABLE 22. Bog Communities.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Ledum—Sphagnum, near Torneträsk	0.077	0.291	5.35	8.01	3
Empetrum—Calluna, Sækkedammen	0.215	0.870	2.26	3.33	3
Empetrum—Calluna, Lyngby Moss	0.625	2.53	4.90	7.17	3
Chamaedaphne bog near Kalamazoo	10.6	42.9	15.1	21.9	3
Sphagnum moor, Maaløv Krat	1.162	4.70	8.71	12.6	3
Carex—Sphagnum, Maaløv Krat	1.536	6.22	9.07	13.1	3
Eriophorum—Oxycoccus, Maaløv Krat	1.774	7.18	10.4	15.1	3
Carex lasiocarpa bog, northern Mich.	100.0	404.7	12.3	18.8	2
Sphagnum—Hylocomium—Hypnum, Maglemose	5.00	20.2	9.43	14.3	2

LEDUM PALUSTRE–SPHAGNUM FUSCUM HOCHMOOR, NEAR TORNETRÄSK STATION, EASTERN LAPLAND. DU RIETZ (1921: 162, TABLE 17). The type is extensive in Lapland. Du Rietz gives data for field layer only, listing 12 spp. in 40 1-sq.-m. quadrats, and in 10 4-sq.-m. quadrats. In every square meter occur *Ledum, Empetrum, Andromeda polifolia, Vaccinium vitis-idaea, V. microcarpum, Betula nana,* and *Rubus chamaemorus. V. uliginosum* and *Pinguicula villosa* are also frequent. Spp. per 1-sq.-m. plot, 9.825; per 4-sq.-m. plot, 10.7; 12 spp. in est. one-piece area of 13.9 mlc. The configuration of plotted points indicates that the species-area curve is already in its convex upper section at 1 sq. m. Extension of the curve leftward results in the extremely small Am value 0.077 mlc., which is only 29.13 sq. dm., or 3.35 sq. ft. If this is not a mistaken value, a "complete stand" (Am $\times$ 20) could be exhibited in a garden plot or museum case 11 feet long by just over 6 feet wide.

EMPETRUM–CALLUNA BOG: SAEKKEDAMMEN, A MOSS IN RUDER HEGN, DENMARK. RAUNKIAER (1910: 83). The location is about 10 miles n.n.w. of Copenhagen. Only 5 species of vascular plants are listed in the 50 0.1-sq.-m. plots of this enumeration. *Empetrum* occurs in all 50, *Eriophorum vaginatum* in 38, *Calluna* in 27, cranberry (*Oxycoccus palustris*) in 21, and *V. uliginosum* in 2. — "Effective plot-size" is estimated at .0875 mlc., with 2.76 spp. per plot. One-piece equivalent of the aggregate is 7.5 mlc. The Am value is about 3 times that of the preceding community.

EMPETRUM–CALLUNA BOG: LYNGBY MOSS, DENMARK. RAUNKIAER (1910: 83). Lyngby is not far n.n.w. from Copenhagen. *Empetrum* is in 47 plots of this enumeration, *Eriophorum* and cranberry each in 48, *Calluna* in 30. *Drosera, Menyanthes,* 3 species of *Carex* in a few plots, and *Scheuchzeria* in 2 plots, complete the list. Spp. per plot, 4.42. Effective plot-size and one-piece equivalent area are as in Sækkedammen.

CHAMAEDAPHNE BOG NEAR KALAMAZOO, S.W. MICHIGAN. L. A. KENOYER (1927: 347). This is the low-shrub zone of a typical peat bog of the vicinity. The survey comprises 25 1-sq.-m. quadrats in line, separated by 4-pace intervals.

It includes density estimates as well as frequency of occurrence in plots. *Sphagnum* sp. is listed as in 23 plots, *Aulacomnium palustre* in 16; these mosses were not omitted from the species-area treatment. *Chamaedaphne calyculata,* the dominant, is in all plots, with 1320 individuals. Herbs of diverse types include a *Sagittaria,* a grass, a rush, 2 *Carices,* the orchid with grasslike leaves *Calopogon pulchellus, Drosera,* a violet, and *Menyanthes. Vaccinium macrocarpum* is in 9 plots, *Solidago* sp. in 12, *Aspidium thelypteris* in 8. The total estimate of individuals is 3242, about 130 plants per sq. m. Spp. per plot average 6.08. Spp. in the 25 plots, 22. Estimated one-piece area is 11.0 mlc. The vegetation is apparently less homogeneous than the north-European bogs. The larger number of species is partly due to the larger area surveyed (5 times the usual Raunkiaer aggregate).

Sphagnum moor, Maalφv Krat, Denmark. Raunkiaer (1910: 81, 83, Table 25, Column 3). Raunkiaer studied bogs of a moor-complex in the Maalφv Krat district south of the west end of Jonstrup Vang (Meadow). These places are also n.n.w. of Copenhagen. The terrain is a high upland dotted with ponds, many of which are excavations for peat. This enumeration is for a quite small *Sphagnum* moor just west of Haven. It is assigned to the *Eriophorum–Oxycoccus* facies. In its highest part are a little *Polytrichum* and *Calluna;* in the surrounding narrow zone are *Hypnaceae* with *Equisetum* and *Carices* but no *Sphagnum* or *Eriophorum.* — The main bog area has cranberry in 41 plots, *Eriophorum vaginatum* in 48, *E. polystachyum* in 23, *Carex stricta* in 26, *C. rostrata* in 23. In all 50 plots are 16 spp. Mean no. of spp. per plot, 5.46. One-piece area equivalent to aggregate is 5.36 mlc.

Carex–Sphagnum moor, Maalφv Krat. Raunkiaer (1910: 80, 83, Table 25, Column 1). This and the next example are parts of a bog which, with two nearby bog areas, is located near the road between Blide and the Ballerup-Jonstrup road. This bog has an upper and a lower border zone, an open-water zone with *Menyanthes,* around the principal raised-bog area designated *Sphagnum* Hængesæk. This itself has three parts: a quaking outer zone, a firmer part in which 50 plots were studied, and the middlemost, somewhat higher part forming the next example. The firm part around the middle is characterized by a combination of 4 species: *Carex rostrata, C. canescens, Agrostis canina,* and *Oxycoccus palustris.* They occur in 50, 36, 39, and 49 plots. The only other species of fairly high frequency is *Peucedanum palustre* in 25 plots. There are 16 spp.; 5.08 per plot.

Eriophorum–Oxycoccus facies, Maal v Krat. Raunkiaer (1910: 81, 83, Table 25, Column 2). This enumeration is in the high central part of the Hængesæk just described. It is assigned to the same facies as that of the *Sphagnum* moor just west of Haven. Of 4 leading species, *Oxycoccus* is in 49 plots, *E. vaginatum* in 46, *E. polystachyum* in 37, and *Carex rostrata* in 36.

Drosera occurs in 24 plots, *Scheuchzeria palustris* in 15, *Andromeda* in 14. There are 18 spp. in all; 5.60 per plot. Equivalent area and effective plot-size are the same in all three Maaløv Krat examples: 5.36 and 0.0618 milacres. This is the richest in species of the European bogs treated.

Carex lasiocarpa bog, Cheboygan County, Michigan. Edith Woollett, Doris Dean, and Helen Coburn (1925). The authors studied species and area in Smith Bog in the north part of the Lower Peninsula, not far from Douglas Lake. A nearly uniform mat of the dominant sedge covered 23,159 sq. m. (5723 mlc.). Double rows of contiguous 1-sq.-m. quadrats were arranged along lines wholly within the *Carex* area. There were 1050 plots (259.6 mlc.). The entire area was searched for species not in the plots, making a total of 29 species. 21 occurred in the plots; mean no. of spp. per plot was 2.65. No other species approached the dominant in frequency (it occurred in all 1050 plots). Some of the others are: *Dulichium arundinaceum* in 390 plots, *Eleocharis palustris* in 380, *Potamogeton heterophyllus* in 240, *E. acuminata* 207, *Juncus crinita* 94, *Lysimachia terrestris* 61, *Potentilla palustris* 51, *Chamaedaphne calyculata* 50. — One-piece area equivalent to the plots was estimated at 285 mlc. There were thus 3 widely separated points through which an S-curve was drawn. The large reference areas resulting are attributed to strong domination by *C. lasiocarpa* and to the persistence into very large areas of about the same rate of addition of species. This rate, though low, continues over the graph in a nearly straight line; it almost maintains a logarithmic rate. This has the effect of determining higher positions on the curve of the two points Ar and Af (smallest and largest of the 3 reference areas).

Maglemose, near Grib Skov, northern Zealand, Denmark. Carsten Olsen (1920). Bryophyte vegetation is presented in detail for 5 groups of 36 0.1-sq.-m. plots; in another set of 121 plots, 6 species of *Sphagnum* are the only plants listed. — Olsen's article is the fifth part of a series of papers on Maglemose; the preceding parts were published together in 1919 in the same journal. The description of higher vegetation by Henning E. Petersen gives enumerations in similar plot-groups (1 of 30, 2 of 64, and 2 of 121 plots) for 8 higher-plant dominants of the bog. In order of importance, they are *Calluna, Eriophorum vaginatum, Empetrum, Oxycoccus quadripetalus, Vaccinium uliginosum;* less frequently, *V. vitis-idaea, Rubus chamaemorus,* and *Andromeda.* — Each plot-group forms a square. Interval between plot-centers is one meter in each direction. The bryophyte plot-group with most species (14) was in Area C. From Olsen's table for it, a map was made of its 36 plots, showing species present in each. There are 4 species of *Sphagnum,* 7 other moss species, and 3 liverworts. *Hylocomium Schreberi* and *Hypnum cupressiforme* each occur in 25 plots, *Sphagnum rubellum* in 18, *Bazzania triloba* 14, *Aulacomnium palustre* 11, *Hylocomium splendens* 10, *S. magellanicum* 7. Spp. per plot, 3.44. — The map made possible a replicated count of species for aggregates of 2, 4, 6, 9, and 18

plots. Two independent methods of estimating equivalent one-piece areas for these aggregates gave fair agreement. The mean equivalent for 9 plots is 1.03 mlc.; for 36 plots it is 4.47 mlc. — It may be presumed that the plot-groups for the moss vegetation were located where higher plants were least prevalent. To the extent that they are present in the plots at Olsen's Area C, they may help to determine an Am-value larger than expected (5 mlc., or 20.23 sq. m.). This is larger than for any other of the European bogs of Table 22, but smaller than for any of the three moss-layer examples in Russian bogs (discussed in later section on mixed types of vegetation). Another likely reason for these large reference areas in moss vegetation is the considerable size frequently attained by many of the moss cushions or mats formed by plants of a single species.

LICHEN AND HERBACEOUS VEGETATION OF ROCKY SURFACES

In many mountain areas and in districts scoured by glaciers, a considerable proportion of the surface is rock, stony debris, or talus. Fragments may be of all sizes from large boulders to fine gravel. All degrees of stability likewise are found, from gravel slides and rock streams (as in the San Juan mountains of southwest Colorado) to firmly interlocked and compacted stony floors of angular fragments. Lichens are the usual plants of exposed dry surfaces. Mats formed principally of mosses are usual on shaded cliffs of humid canyons. Mixed-herb assemblages or inceptive grasslands develop in loose or compacted fragmented debris. While shrubs and trees may be early invaders, and may even assume dominance shortly after a surface is bared (as in some chaparral districts), their communities are not very different from other shrub and forest types.

TABLE 23. Lichen and Herbaceous Vegetation of Rocky Surfaces.

Stand or type	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Parmelia omphalodes, Jungfrun	0.1355	0.548	11.3	16.3	3
Same, halophyte variant	0.1275	0.516	12.3	17.8	2
Lecanora deusta, Jungfrun	0.0235	0.0951	8.05	11.7	1
L. quartzina, upper variant	0.0738	0.299	6.31	9.12	3
L. quartzina, lower variant	0.105	0.425	3.66	5.30	3
Cladonia, shaded talus, n.e. Minn.	0.137	0.554	8.45	16.9	3
Arête de Sandgrat	4.27	17.3	15.4	22.6	2
Pierrier de Sandalp	18.5	45.7	27.0	39.2	2
Stipetum, sunny talus, Alps	22.4	90.8	21.3	31.4	2
Herbs, s. Alps border.	14.0	56.8	25.3	37.8	3

PARMELIA OMPHALODES ASSOCIATION, ISLAND JUNGFRUN. DU RIETZ (1921: 164, TABLE 21, FIG. 19). The coasts and islands of the Baltic afford much rock surface on which lichen covers are well developed. Du Rietz studied several lichen groupings, especially on Jungfrun. The brown foliose *Parmelia omphalodes* is clearly dominant in one of the more extensive types. In Du Rietz's plots

it covers half of the surface. The most frequent other species are *Cladonia squamosa* f. *muricella, Lecanora polytropa, C. Floerkeana* f. *carcata, C. coccifera* v. *stemmatina, Gyrophora polyphylla, P. fuliginosa, P. saxatilis.* The HAUPTVARIANTE has also 2 moss species in small numbers, and higher frequencies of *P. physodes,* and of a form of *C. gracilis;* while the HALOPHYTENVARIANTE has more of *Lecidea neglecta, P. conspersa, P. Mougeotii, Ramalina subfarinacea,* and *Rhizocarpon constrictum.* For the main variant, Du Rietz listed species in 10 16-sq.-m. quadrats, well dispersed in the lower part of the island, all on moderately exposed rocks. Each large quadrat was subdivided into 4- and 1-sq.-m. plots. The halophyte variant is at the upper edge of the *Sturmgürtel,* on rocks strongly exposed to wind and salt spray. There were many plots in this variant, located on different sides of the island. The 9 plot-sizes range from 1 sq. centimeter to 15 sq. meters. The large number of species recorded, 61 in all, is due to considerable variability of site, to scattering of the many plots, and to thoroughness of the survey of an inherently rich community. Dispersal and variability do not affect the species-area results, which are based only on average numbers of species per plot. Du Rietz summarizes these numbers on p. 207 in Table 32. Some of these are, for halophyte variant: 2.13 spp. in 4 sq. cm., 5.40 in 100 sq. cm., 9.22 in 400, 15.37 in 2500 (.25 sq. m.), 18.44 in 1 sq. m., 23.3 in 4, and 29.0 in 16 sq. m. A smooth S-curve based on these numbers fits the smaller areas well, the larger areas rather poorly (else a dependability rating "1" might have been justified). Du Rietz presents on p. 206 an interesting figure for this halophyte variant and 2 other lichen communities. Logarithm of average species-number per quadrat is plotted against logarithm of area. The decline in rate of species-increase as area is enlarged, is emphasized in his discussion. The preceding figure (p. 205) shows similar graphs for four communities (pine–dwarf-shrub, and heath). — Returning to the Hauptvariante in *Parmelia omphalodes* association, species numbers are: 17.58 in 1 sq. m., 22.29 in 4, 27.7 in 16 sq. m. The trend of its S-curve was judged largely from that of the halophyte variant.

LECANORA DEUSTA ASSOCIATION, JUNGFRUN. DU RIETZ (1921: 168, TABLE 23, FIGURE 19). This community is fairly extensive and characteristic on driest upper surfaces of rocks on the east coast of south Sweden and the many islands that fringe it. In its Jungfrun sites, the dominant lichen, a blackish crustose species, usually covers about 90% of the surface. Rarely does any of its companion species cover more than about 6%. The more frequent species are: *Lecidea furvella, Gyrophora polyphylla, Parmelia omphalodes* (dwarfed form), *Lecidea neglecta, Rhizocarpon geographicum, R. atrovirens, Lecanora polytropa, Cladonia coccifera* var. *stemmatina,* and *C. Floerkeana* var. *carcata.* The survey covers 10 16-sq.-m. plots (divided into meter squares), also 20 4-sq.-m. plots (divided into meter squares, and these into 0.25-sq.-m. and still smaller squares down to 1-sq.-cm.). In all, 48 spp. are recorded. — For 5 of the 9 plot-sizes, mean

nos. of spp. per plot run: in 1 sq. cm. 2.35 spp., in 25 sq. cm. 5.01, in 4 sq. dm. 9.73, in 1 sq. m. 15.6, and in 16 sq. m. 20.9 spp. The species-area curve fits the points fairly well, missing two of them by 0.7 species. It is a less steep curve than that for either variant of the *Parmelia* association, with more species at small areas, fewer at areas greater than 0.1 sq. m. In spite of the strong dominance of *L. deusta,* the smaller size of individual thalli in this more xeric site permits better representation of species in areas of a square foot or smaller. The less exposed site in which *P. omphalodes* dominates is perhaps the reason for its maximum floristic richness. Both the richness (with which steepness of the *Parmelia* curve is correlated), and the larger average size of plants, cause reference areas for both *P. omphalodes* variants to exceed those for *L. deusta* (Am-values are .548 and .516 sq. m. as contrasted with .0951 for L. deusta). One expects the lichen associations to have smaller minimum areas than any other types: the smallest heretofore has been .291 sq. m. for Du Rietz's near-arctic bog at Torneträsk. Of the 6 lichen communities treated, only *L. deusta* has a smaller Am value. A "complete stand" for L. deusta would cover 1.9 sq. m. or 0.47 milacre or 20.5 sq. ft., with 16 spp. The flat top of one large boulder could represent the association adequately.

Lecanora quartzina association of the Sturmgürtel, Jungfrun. Du Rietz (1921: 171, Table 25, Fig. 19). This conspicuous yellow-green maritime rock-lichen dominates a narrow band just below the middle of the range of levels reached by waves during storms. Its maximum width is several meters; its lower part is differentiated somewhat from the upper. Du Rietz had difficulty finding large enough homogeneous areas in either variant. In the 15 1-sq.-m. quadrats of the lower-level variant, 9 species are recorded; in the same-sized upper-level aggregate are 16 spp. Three lower-variant species are not listed in upper-variant plots. The 7 plot-sizes range from 1 sq. cm. to 1 sq. m., but the 2 variants are not separated in the sizes below 1 sq. m. Curves for the variants were each based on only two points: one for mean no. of spp. per 1 sq. m. plot (6.07 for lower and 11.07 for upper), the other point for total no. of spp. (9 and 16) in one-piece area equivalent to each 15-plot aggregate. This was estimated at 18.07 mlc. Though dependability of the curves is low, results are in accord with expectations from comparison with the other lichen types. The Am values should be smaller than those for the *P. omphalodes* type because of the smaller plants in the Sturmgürtel. Am values should be larger than in the *L. deusta* type if, as is likely, the plants are on the average less minute.

Cladonia community, shaded block talus, northeastern Minnesota. Bruce Fink (1903). Fink studied lichens of cliffs along the north shore of Lake Superior. In 1897 he saw extensive talus areas of huge blocks of rock covered with larger Cladonias; "one such field covered more than an acre." In another talus about 1 mile w. of Grand Marais Bay, below the north-facing cliff called Howenstine Bluff, F recorded the species on 1 sq. rod of various-sized

blocks. The talus is 45 ft. high, with 35° slope. Trees of moderate size shaded all but its upper part. 21 species and varieties of *Cladonia* covered the plot. *C. gracilis* and its var. *dilatata* were especially abundant. *C. cristatella, C. verticillata* and a variety of it, *C. furcata paradoxa, C. fimbriata* and 3 varieties, and 5 other species were all "common enough." (Of the remaining 6 spp., *C. rangiferina, C. alpestris,* and *C. sylvatica* were the leading spp. in the other notable lichen types of the district.) — On the Howenstine talus were scattered logs on which smaller *Cladonias* were frequent. Fink thought it likely that the area had been burned (possibly 30 years earlier) and that the lichens had developed since. One of his photographs (Fig. 2) shows one square foot "with a dense growth of *C. gracilis* and 8 or 9 other *Cladonias* in small numbers." — If we consider that 19 kinds of *Cladonia* on 1 square rod and 8 kinds on 1 square foot are somewhat more representative of the general condition of this lichen cover, the 2 points so determined are available for a tentative species-area curve. A square rod (16.5 feet square) is 6.25 milacres; 1 sq. ft. is .02295 mlc. A likely position for the curve puts the flex point at about .025 mlc. The Am value from the curve, 0.137 mlc. or .554 sq. m., is slightly larger than that of Du Rietz's *Parmelia omphalodes* association (Hauptvariante).

Arête rocheuse de Sandgrat, "hautes Alpes," elev. 2780 m. Jaccard (1914: 16, Table 2). Jaccard described this as an example of an extreme site excluding all but a few species, making it possible for two plots to have identical species lists. The area examined had 24 species; 21 of them occur in one group of 12 contiguous 1-sq.-m. plots; plots 4 and 5 have the same 11 spp.; plots 6 and 7 have the same 10 spp. Species occurring on all 12 plots are *Alsine Cherleri, Chrysanthemum alpinum, Cetraria islandica, Gentiana bavarica,* and *Luzula spicata. Silene exscapa* is in 11 plots, *Saxifraga bryoides* in 10, *S. exarata* in 9, *Potentilla frigida* in 8. — In 1-sq.-m. plots, av. no. of spp. is 11.0; combinations of neighboring plots gave 13.36 spp. in 2 sq. m., 15 in 3, 16 in 4, and 18 in 6. The 7 available points determine the lower section of an S-curve. Its slope is moderate because rate of increase is low, and because, with plants small and not crowded, number of species per plot is relatively high at small areas. Reference areas are small as compared with floristically rich rocky areas, such as Jaccard's plot-group III in the Pierrier de Sandalp, and his *éboulis morainique* in the same district.

Pierrier de Sandalp, Linth valley, Alpes Glaronaises, elev. 1938 m. Jaccard (1914: 6-9, Table 1). The site is a fairly old alluvion or terrace of large pebbles, on one side of the Linth River, 1 to 2 meters above the torrent. It is over 200 m. long and about 30 m. wide. Its cover is a mixture of many herbs, mostly perennial, including 8 grass species. A moss and 3 *Salix* species are also among the 70 species recorded in the whole area examined. Detailed listings were made for four groups of 1-sq.-m. plots; the groups are separated by gaps of 5, 20, and 50 m. Groups I, II, and III are much alike; IV has a sparser cover

and is on a deposit not so old as the main part. (It was not included with the others in the species-area treatment.) The apparently stable cover is principally of the characteristic and generally-distributed perennials *Anthyllis vulneraria, Epilobium Fleischeri, Gypsophila repens,* and *Linaria alpina.* Others include *Euphrasia salisburgensis, Kernera saxatilis, Festuca pumila, Oxytropis* (2 species), *Poa alpina, P. minor, Saxifraga aizoides.* Most of these are on fewer plots in plot-group IV. — For the 4 sets of plots, pertinent figures are summarized thus:

Group	Area, sq. m.	Spp. per plot	Total spp.
I	19	4.37	19
II	21	7.05	32
III	18	9.61	36
Mean	19.33	6.97	29
IV	27	2.81	19

In addition, there is a total of 45 species in the 58 sq. m. of the aggregate of the 3 plot-groups. The estimated one-piece equivalent of the aggregate is 43.1 mlc. — The Am-value, 18.5 mlc., is in the range of sizes found for more open grass lands. In this case, it is likely that competition among plants of the pebbly terrace does not exclude immigration of almost any species from surrounding communities. Jaccard pointed out that the species present are a chance selection from the available flora, and that they show no particular adaptation to the site. These circumstances are in accord with a species-area curve which is only moderately convex in its upper part: the rate of species-increment persists well into rather large areas.

A tentative curve drawn for plot-group IV, though based on insufficient data, suggests an Am of 24 mlc. (59.4 sq. m.), Sm of 25.4. This result is expectable, because of the sparser plant cover and scantier flora as compared with groups I to III.

Jaccard briefly describes also the debris-slope (30 to 35°) which he calls the PIERRIER D' ÉBOULIS MORAINIQUE, less than 1 km. from the Linth River terrace. The list of species is much the same. He studied a homogeneous area of 40 sq. m. in which species-numbers per sq. m. were 8 to 13, and in which the first 13 plots showed 28 spp. A tentative curve for the éboulis gave a likely Am of 18.1 mlc. (44.8 sq. m.), with 40.6 species.

STIPA CALAMAGROSTIS ASSOCIATION OF SUNNY TALUS SLOPES, GLARNER ALPS. HANS JENNY (1930: 164-178, TABLE 1, FIG. 8). This community is found on south and southeast slopes in calcareous districts at moderate elevations (Montane Zone). It is a heterogeneous assemblage of species; rock-plants, ruderals, plants of forest and shrubby borders, of sparse and stony grasslands. The characteristic species are *Stipa, Vincetoxicum officinale, Galeopsis angustifolia, Reseda luteola, Epilobium rosmarinifolium,* and *Calamintha nepetoides.* Many of the other species occur also in the rocky or stony grasslands of the southern

base of the Alps (as in the next example from Jäggli and Jaccard). — Jenny gives a detailed association table, from which 7 Aufnahmen for stated areas were used to make a composite species-area curve for the type. One other area, No. 4, approaching optimal phase of development, is much richer in species composition than the 7 chosen; 3 areas, Nos. 6, 7, and 10 are obviously poorer in species. It was found that the different Aufnahmen could not be divided into two or three groups which agree within themselves as to texture of rock fragments, stage of development, elevation, location, and degree of instability of surface materials. (Elevations range from 480 to 900 meters; most of the slopes still move somewhat; steepness is 30 to 36°; extent of the Aufnahmen varies from 16 to 100 sq. m.) — Species-numbers at small areas were found by subdividing Jenny's map of a 15-sq.-m. plot. This is his Fig. 8, p. 176, showing the condition in 1926; the plot is on a slope laid bare in 1919 by a rock-slide. The map shows individuals of 19 species. Some of the species numbers used for plotting are:

Milacres	0.232	0.926	3.95	12.35	24.71
Species	4.56	11.25	21	26	32

The Am value found is large: since usually less than one-fourth the surface is covered by plants, the same number of species might be found in one-fourth as much area if occupation were nearly complete. It may be presumed that reference areas will be progressively reduced as (or if) the vegetation is able to develop into a continuous cover of some type other than the Stipetum.

Some of the other rock communities in Jenny's article are equally worthy of species-area study. His bibliography includes citations of many other fine studies of the vegetation of cliffs and debris slopes.

Herbaceous vegetation of rocky and thin-soiled sunny slopes, Ticino and Lombardy. M. Jäggli (1928), and P. Jaccard (1914). Jäggli describes Monte di Caslano, a bold rocky hill nearly surrounded by a western arm of Lake Lugano. On the steep slopes to the lake on south and southeast sides, with dolomite substratum, the nearly bare surface is strongly insolated. On a plot of 4 sq. m. in the *vegetazione rupestre,* Jäggli listed 5 moss species and 16 flowering-plant species. All the mosses and 8 other species are marked as characteristic of rocky sites. These 8 are *Sesleria coerulea, Carex humilis, Dianthus Caryophyllus, Fumana ericoides, Thymus Serpyllum, Teucrium chamaedrys, Globularia cordifolia,* and *Leontodon tenuiflorus.* A supplementary list for similar sites nearby names 7 more species. — A grassland, sparse and xeric, covers about a third of the dry south and southeast sides in small areas among rocks and among shrubs and stunted oaks. In some places this *praterie magre asciutte* appears to be stable. Especially where it is well enough developed to make the cutting of wild hay feasible, this practice tends to prevent replacement by the *boscaglie xerofili.* Jäggli's example of this praterie, recorded in August, 1927, covers 50 sq. m. on a 28° slope facing southeast. Soil is coarse and shallow (10-15 cm.). The plants are mostly herbs, with a few suffrutices and suffrutescent herbs. Of

the 37 species scattered sparsely over the area, 5 grasses, a sedge, and a lily are fairly numerous. They are *Bromus erectus, Andropogon Gryllus, Carex humilis, Molinia coerulea, Sesleria coerulea, Anthericum ramosum,* and *Brachypodium pinnatum.* This list of 37 species includes 9 of the 16 species of the 4-sq.-m. rock plot, suggesting close kinship of rock vegetation to praterie. A supplementary praterie list gives 27 other species in similar sites on the same part of Mt. Caslano. — Jäggli relates this inceptive grassland of rocks and thin-soil slopes to the Xero-Brometum erecti described by J. Braun in the southern Cevennes, and names species common to both.

A grassland described by JACCARD (1914: 19) as a very dry and meager prairie is situated ABOVE MENAGGIO on Lake Como (only about 17 miles e.n.e. of Mt. Caslano). The soil is shallow. A few moss species and *Festuca ovina capillata* form the chief cover. *Bromus erectus, Sesleria, Danthonia procumbens, Carex Baldensis,* and many herb and some few low-bush species are scattered sparsely through the area. Jaccard lists 32 species on a 25-sq.-m. plot. Some few of these are the same as at Mt. Caslano: in more cases the same genera are common to both localities. It seems that the 3 plots are nearly enough of the same type to be used together for a species-area curve. The Am-value found, 14 mlc., is fairly large. This is an expectable consequence of the incompleteness of the plant cover and the rich supply of species in surrounding areas. Jaccard says the prairie above Menaggio is a peculiar association of species which, generally, occupy habitats that are very different.

ALVAR VEGETATION, AND OTHER HORIZONTAL ROCK-BARRENS. It is regretted that examples of these types are not included among those here studied. Alvar is the name for bare or very thinly-covered outcrops of calcareous rock, best developed in islands of the Baltic Sea, especially Öland. The first plants are lichens, with various crevice-plants in the joints. These rock-pavements and the concomitant development of soil and of vegetation over them have been well described by C. FERDINANDSEN (1916), by Du Rietz, and others.

STRATIFIED COMMUNITIES; MIXED VEGETATION AND COMPLEXES COMPRISING UNLIKE GROWTH-FORMS

It is not profitable to attempt a sharp distinction between stratified compound vegetation in which at least the top stratum is apparently homogenous, and mixtures or complexes in which horizontal discontinuity is obvious. A conspicuous example of such a mixture is that of the Boulder mesa-top, next described. Three forests with their strata illustrate some of the complexities of the familiar type. The moss, dwarf-shrub and (usually scattered) pine components of raised bogs in Russia, followed by relatively simple two-phase mixtures of bushes or shrubs with grass or herbs, conclude the series of vegetation-units treated in this article.

TABLE 24. Vegetation Complexes of Unlike Growth-Forms.

Complexes and their components	Am, *mlc.*	Am, *sq. m.*	Sr	Sm	D
Mesa-top near Boulder:					
All species	24.9	101	26.25	37.7	1
Woody species	198	802	9.89	15.0	1
Herb species	10.6	42.9	16.2	24.2	1
Mixed decid. forest, Indiana:					
All species	226	913	59.4	89.4	2
Trees alone, 3″ +	1 665	67 380	14.25	20.7	3
Shrub species	195	790	8.73	13.05	2
Herb species, including ferns	199	805	33.8	50.9	2
Conifers + decid., Maine:					
Trees, 3-inch diam. +	519	2 100	8.00	12.05	3
Trees, 1-inch diam. +	225	910	9.45	14.2	3
Shrubs	142.5	577	7.68	11.5	3
Herbs	12.1	49.0	15.0	22.3	3
White pine forest, Wis.:					
Trees, 3-inch diam. +	860	3 480	5.79	8.44	1
Herbs + small woody plants	6.09	24.6	24.6	37.8	3
Herb species	5.85	23.7	16.7	25.0	3
Raised bogs, central Russia:					
Rubskoje Moor, field layer	21.6	87.5	8.57	12.7	2
moss layer	6.35	25.7	2.36	3.44	2
Krupino Moor, field layer	7.11	28.8	6.14	8.93	3
moss layer	12.6	51.0	3.00	4.52	2
Mironowo Moor, moss layer	10.5	42.5	3.81	5.70	3
Sagebrush—grass, N. D.:					
Grassland with *A. cana*	10.8	43.7	33.8	49.2	3
Grassland without *A. cana*	8.48	34.3	33.6	48.9	3
Short-grass—bush, Colorado:					
Grassland with bush	7.14	28.9	22.7	34.0	2
Bush phase	2.77	11.2	2.59	3.94	2
Grass phase	8.13	32.9	20.3	29.9	2
Bush—short-grass, S. L. V.:					
Bush with grassland	101	408	22.65	33.05	3
Chrysothamnus—Gutierrezia	27.0	109	3.93	5.73	3+
Short-grass phase	125.5	506	18.7	27.2	3
Bush—grass garigue, France:					
All species	5.135	20.77	26.4	38.8	3
Bush phase	6.65	26.9	10.8	15.8	3
Grass and herb phase	4.315	17.45	15.6	23.1	3
Creosote-bush with herbs:					
Woody spp.: C. V.	1 908	7 721	3.63	5.32	3
G. V.	530	2 145	1.58	2.29	3
Herb spp.: Coachella Valley	1.93	7.81	18.0	25.7	3
Gila Valley	2.45	9.91	16.7	24.0	3

MIXED VEGETATION OF MESA-TOP NEAR BOULDER, COLORADO. VESTAL, SEPTEMBER, 1944. This complex can be described as rock lichens + inceptive grassland + mountain bunch-grass + dwarf-shrub + shrub + foothill conifers (here mostly stunted). Descriptions of these components are included in three papers (Vestal 1914, 1917, 1919). The place studied is near the northwest edge of Horse Mesa, one of the several high "mesas" south of Boulder. (These are

sloping high terraces with thick cap of rocky alluvium). The location is above and a few hundred feet south of Bluebell Spring (which is in Bluebell Canyon). These mesas and their partial cover of rock pines (*P. ponderosa* var. *scopulorum*) were the subject of early papers by RAMALEY, DODDS, AND ROBBINS (UNIV. COLO. STUDIES, VOL. 6, 1908). One part of the very rocky mixed area here treated was mapped in 1919 and at two later times. It is a grid of 42 10-foot squares, and includes a few old but not large pines and numerous small pines dating from about 1883. For more intensive study of the herb and dwarf-shrub vegetation in 1944, a grid of 52 5-foot squares north of the mapped area was used. It included 3 pines 1.5, 2, and 4 feet high, with a few seedlings and 5 stumps (the largest 6.5 inches in diam.), and 1 small tree (6.5 feet) and 1 3-inch seedling of *Pseudotsuga taxifolia*. *Juniperus sibirica* was represented by mats or seedlings in 15 of the 52 squares: *Arctostaphylos uva-ursi* in 19 squares; the spiny dwarf-shrub *Ceanothus Fendleri* in 7; small individuals of *Rhus glabra, Prunus melanocarpa, P. pennsylvanica,* and *Rubus deliciosus,* in 5, 2, 1, and 1 of the 52 squares. Most of the herbs had higher frequencies. Worthy of mention are *Andropogon scoparius, Muhlenbergia gracilis,* a *Carex, Koeleria, Danthonia; Artemisia, Chrysopsis, Aster, Penstemon, Comandra, Sedum.* The lichens on surface rocks and boulders were omitted from the count, but mosses (a *Polytrichum* or closely-related moss, and a *Grimmia*), were included. They were usually on the soil itself, either at the north base of rocks or in places subject to erosion (they tend to retard surface washing). In one square *Polytrichum* covered 160 sq. inches.

From the detailed table made in the field, various combinations of plots were made, giving species-numbers for 14 plot-sizes (1 to 52 squares). To give data for larger sizes, treeless parts of the older grid, and another treeless and very rocky area south of the older grid were searched for additional species. Area 1 + Area 2 make 196 squares; 1 + 2 + 3 make 340 squares. Translated to milacres, part of the array of areas and species-numbers (with mosses included in "all species") appears as follows:

Milacres	0.57	1.15	2.30	4.59	7.46	14.9	29.8	112.5	195.1
Woody spp.	1.25	2.10	3.15	4.25	5.25	7	9	13	16
Herb spp.	9.35	13.04	16.45	20.4	22.4	25	26	37	41
All spp.	10.75	15.44	20.22	25.7	29.1	34	37	52	59

From these figures, S-curves were made for woody species alone, herb species alone, and for all species. The resulting Am, Sr, and Sm values appear in Table 24. For either woody species or grassland, the reference areas are several times as large as they would be if other growth-forms were not present. In places, especially near the edge of the mesa-top, sizable boulders cover almost half the surface. Whatever space is occupied by actual trees or tree-clumps is likewise unavailable to shrubby cover or to grassland.

The components of this mosaic are prominent among those encountered over the gravelly or rocky surface of the granite foothills and lower mountains of

the Colorado Front Range and other parts of the Southern Rocky Mountains. The complex is thus fairly typical of the lower yellow-pine zone in those areas that are neither grassland nor actual forest. Aggregate area of this mosaic probably exceeds 2000 sq. miles. Similar mixtures with some of the same components cover much wider areas in the mountains of the west.

Mixed deciduous forest: trees, shrubs, herbs. Nash's Woods, Posey County, s. w. Indiana. S. A. Cain (1934). The location is 5 miles s. e. of New Harmony. In a 45-acre stand, 25 acres of old-growth forest are dominated by *Liriodendron, Quercus alba, Acer saccharum,* and *Nyssa sylvatica. Fraxinus lanceolata, Ulmus fulva; Sassafras, Cornus florida,* and *Cercis* are numerous. Shrubs and vines are well represented; 7 ferns and many herb species form the ground cover. In each of 25 places, Cain established plots of 6 sizes: 1, 2, 4, 25, 50, and 100 sq. m. These were later supplemented by 9 and 16 sq. m. From Cain's frequence table on pp. 542-44, separate data were taken for trees, shrubs, herbs including ferns, and totals for all species. Mean number of species per plot for each group was found from frequencies (by finding the total number of "occurrences" and dividing by number of plots, 25). For areas larger than 100 sq. m., the number of shrub or of herb species in an aggregate of 25 plots was the basis for an estimate of the somewhat smaller number of species in a single compact area of the same extent as the aggregate. Also, the larger one-piece area having the same number of species as an aggregate, could be estimated (I-conversion).

Since the frequencies for tree species included small sizes, conversion was essayed to give data for trees of 3-inch diameter and larger. For such trees, the density was assumed to be 136 per acre. A table was prepared showing number of plots of three sizes in which each tree species occurred (the sizes: 1, 25, and 100 sq. m.). A column was added for likely number of individuals to give the stated number of occurrences. Thus for 28 tree species represented in 25 100-sq.-m. plots by 377 occurrences, a likely number of individual trees of all sizes was estimated to be 1054. For trees 3″ or larger on the same plots, the likely number is 84 (from density of 136 per acre on .6178 acre). Likely numbers for trees of particular leading species were suggested from data given on Cain's p. 556; for the other species from the table of occurrences. A second table of occurrences was prepared for the 84 trees 3″ and larger. About 18 species are represented by these 84 individuals. Av. no. of spp. per plot (again from no. of occurrences), comes to 0.8 in 25 sq. m., 2.96 in 100 sq. m. In the aggregate of 25 1-sq.-m. plots there are 2 spp.; in the 25-sq.-m. plots, 12 spp.; in the 100-sq.-m. plots, the 18 spp. mentioned. From species-numbers thus roughly approximated, an S-curve was made. It gave the Am value of 1665 milacres. (This compares with 1428 to 2761 for other old-growth mixed forests in Indiana: see Table 2 in this article.)

For the shrub and vine species, the herb species, and the complete list of

species, it was relatively simple to find species-numbers for the various plot-sizes, and to make a species-area curve for each group of species. The curve for shrubs and vines is not the same as a curve for all plants of the shrub stratum, since many young trees are part of that stratum. Similarly the herb group does not include the tree seedlings and low shrubs which form part of the field layer. Probably the rather large reference-areas for the herb group is partly due to this intermixture of woody plants, as well as to complete occupation of part of the ground-space by solid thickets of shrubs or young trees. The minimum area for herbs is 199 milacres, as compared with an ordinary range of 48 to 81 for herb ground-cover under forest (see Table 19). This Am value for herbs of Nash's Woods is larger than that for the shrub group, which is 195 milacres, a result that could hardly be foreseen. (This difference cannot be depended upon, as the error of determining Am for either group of species is probably any amount up to about 20 milacres.) The shrub Am value, 195 milacres, compares with an ordinary range of 46 to 96 milacres, with larger extreme values 198 to 450 (see Tables 11, 8, 20).

One may ask whether a composite curve for plants of such greatly differing size and character as mature trees, tree seedlings, shrubs, tall and low herbs, with areas computed from the curve, can have any real meaning. The author does not see any significance therein; his objective was to find how a composite curve compares with curves for constituent parts of the forest. In making the composite curve, one had to decide whether to use data for all trees or only for the large trees. It is obvious that for a forest which includes many seedling and small trees, omission of an important part of the lower strata would seriously distort representation of the forest as a whole. Therefore the original given data for trees were used. As might be expected, reference areas for all plants in combination prove to be somewhat larger than for either shrubs or herbs, but much smaller than those for the sizable trees.

Mixed conifer–hardwood forest (fir–red maple–spruce), n. Oxford County, w. Maine. H. J. Oosting and J. F. Reed (1944). The type locally designated spruce flat, occupies well-drained, moist soils near streams. The stand studied is at lat. 44° 38′, near Andover, and adjacent to Horseshoe Brook. It has been cut several times, last in 1924; age of larger trees averages 57 years. Dominant trees are *Abies balsamea, Acer rubrum, Picea rubens,* and *A. saccharum. Tsuga canadensis* and *Pinus strobus* are sparingly present. *Acer spicatum, Betula lutea,* and *Fraxinus americana* are abundant in the second story; the ash is growing into the top stratum. Tall shrubs, especially *Corylus rostrata, Alnus incana,* and *Hamamelis virginiana,* occur with the sub-dominant or second-story trees. Other shrubs include species of *Cornus, Viburnum, Rubus, Ilex,* and *Lonicera.* Characteristic herbs are *Trientalis, Oakesia sessilifolia, Cornus canadensis, Maianthemum, Lycopodium* species, and *Clintonia.* — The stand was sampled in 10 places, each with 3 plot-sizes: 100, 16, and 1 sq. m.

Trees 1″ + (one inch diam. and larger) were recorded separately for top story and second story. In all, 673 trees comprised 16 spp., with 7.4 spp. per 100-sq.-m. plot. Young trees 1 to 10 ft. tall, tree seedlings under 1 foot, and shrubs (10 spp.) were recorded from 10 16-sq.-m. plots; herbs (18 spp.) from 10 1-sq.-m. plots. Relatively simple adjustments of data were required for trees 1″ +, and for shrub and herb components, to make species-area curves possible. For trees 3″ +, relative densities were employed. Density of top-story dominants (given on p. 195) comes to 238, and of subdominants (p. 196) to 435, in 1000 sq. m. This makes 673 trees in 247.1 mlc. or 2746 trees 1″ + per acre. If it is assumed that somewhat less than half the dominants have reached or exceeded 3″ diam. (few can have grown much larger), a tentative ratio of trees 3″ + to trees 1″ + is 108 to 673, or 0.1604. From this, the density of 3″ + trees should be 482 per acre. One can now tabulate tree-numbers of the two diameter-limits for different plot sizes (7 were used), and one can also put down for trees 1″ + the number of species at each plot-size, as read from the species-area curve for those trees. Then by C-conversion (use of species-individuals curves) one finds approximate no. of species for the no. of trees 3″ + at each plot-size. This gives data for a species-area curve for trees 3″ +. Reliability of reference areas from such a curve is low, but a rough comparison with the tree-layer of other forests is thus made possible.

Some of the species-numbers for groups of species and for layers are shown in the accompanying table. 38.97 mlc. is the compact area equal to the aggregate of 10 16-sq.-m. plots; 71 mlc. is the est. 1-piece equivalent of the same aggregate (equiv. in having the same no. of spp.); 450 mlc. is the est. 1-piece equiv. of 10 separated 100-sq.-m. plots. Note that line c, for trees 1″ +, may also serve for the tree-crown layer (perhaps the figures should be slightly enlarged to include tallest shrubs accompanying second-story trees). Note also that line g, for trees of all sizes, is not the sum of c, e, and f.

TABLE 24a. Approximate Species-Numbers at Certain Areas, Spruce Flat.

Area in milacres	0.247	3.897	38.97	71	450
a. Herbs	6.0	17.3	26.7	28.5	33.0?
b. Shrubs	1.7	2.8	8.5	10.0	13.6
c. Trees, 1″ +	0.4?	2.3	9.0	10.9	16.0
d. Trees, 3″ +	0.1?	1.3	5.2	6.9	11.8
e. Tree seedlings, < 1 ft.	2.5?	4.9	8.5	9.0	17.5?
f. Young trees, 1-10 ft.	1.1?	3.7	6.0	7.0	17.0?
g. Trees, all sizes	2.6?	5.2?	9.5	11.0	19.0?
h. All species (a + b + g)	10.3?	25.3?	44.7?	49.5?	65.6?
i. Herb layer (a + e)	8.5?	22.2	35.2	37.5	50.5?
j. Shrub layer (b + f)	2.8?	6.5	14.5	17.0	30.6?

The table shows how much the tree seedlings and young trees contribute to herb and shrub layers. The question is raised: Which is the real synusia or component of a several-layered stand, the group of species of one growth-form, or

the layer? A group of similar species, such as coniferous trees, usually takes up space in more than one layer; a layer (except the topmost) comprises one or more components which attain maturity in that stratum, plus young plants which will later belong in a higher stratum. Or does each group of species form different synusiae in different layers? No answer will be attempted to these questions. Students of vegetation have become increasingly aware of the very great complexity of a mixed forest; the situation just posed is merely another example of that fact.

In considering the minimum areas found for different elements of the mixed spruce stand as shown in Table 24, one notes that the Am value for trees 3″ + (519 mlc.) is smaller than that of any high-density deciduous stands of Tables 2 and 3, such as Potzger's No. 39 (868 mlc.) and McCoy's stands I and V (718 and 799). In general, stands of conifers or of conifers with slow-growing hardwoods have higher densities and smaller reference areas than deciduous stands. This same Am of the spruce flat likewise is smaller than that of Potzger's northern pine forests (678 and 860 mlc.) This is likewise expectable in a cut-over stand of young trees as compared with old-growth stands. — The minimum areas for shrubs in the spruce flat (142.5 mlc.) and in Nash's Woods, Indiana (195 mlc.) are larger than in a majority of bush and shrub types of treeless areas. — The very small Am value for herb cover in the spruce flat (12.1 mlc.) as compared with ordinary range of 48 to 81, from Table 19, suggests that the 1-sq.-m. plots may represent local patches of pure herb cover rather than average condition of the forest floor.

White pine forest, Vilas Co., n. Wisconsin. J. E. Potzger (1946: 225). The trees of this notable stand, mostly *Pinus strobus,* on the property of the Dairymen's Country Club, between Big Crooked and Wolf Lakes, have already been included in the section on forests of middle latitudes. Potzger's Table 23 gives details of density and frequency for plants of the ground cover, in 20 1-sq.-m. plots. There are 26 herb species, of which *Maianthemum, Waldsteinia, Trientalis,* and *Pteridium* are most abundant and frequent. Tree seedlings of 8 species occur. Only *Acer rubrum* and *A. saccharum* are important. A relatively small number of young or small shrubs in 5 species brings the list for the 20 plots to 39 species. — The average number of species per plot is for herbs 6.65, for tree seedlings 2.25, for shrubs 0.5, for all three groups 8.95. The one-piece area estimated to be equivalent to the 20 plots is 7.17 milacres. Two species-area curves were made, one for the low-plant layer as a whole (the 3 groups of species), the other for herb species.

Comparison of ground cover in this forest with that of either Nash's Woods (deciduous) or the conifer-deciduous mixture in Maine seems not to be feasible. Such comparisons probably must await new field studies especially designed for the purpose.

Three-layered raised bogs, central Russia. N. J. and S. Katz (1926:

190-191). The authors investigated Minimiareal after the methods of Du Rietz "auf den Hochmooren Mittelrusslands weit verbreiteten Assoziationen der Torfmoosreichen Zwergstrauch und Gras-Nadelwälder *Pinus silvestris–Cassandra calyculata–Sphagnum recurvum* und *Pinus silvestris–Eriophorum vaginatum–Sphagnum recurvum*. . . ." The two associations were each studied in 3 localities: Rubskoje Moor (farthest east) in Govt. Iwanowo-Wosnesensk, Distr. Tejkowo; Krupino Moor, 336 km. w. s. w. of Rubskoje, in Govt. Moscow, Distr. Wolokolamsk; and moors between Mironowo and Saprudje in Govt. Moscow, Distr. Leninsk. This location is 150 km. from Krupino, and 200 km. from Rubskoje. Separated quadrats of three sizes, 1, 4, and 16 sq. m., are summarized in the authors' tables. Pines of tree size are listed in from 71 to 91% of the 1-sq.-m. plots in all six sets of data. In both associations the dwarf shrubs are *Vaccinium* spp. (*V. oxycoccus* most frequent), *Cassandra, Ledum,* and *Andromeda.* (Most botanists use for *Cassandra* the genus name *Chamaedaphne.*) Small pines are frequent in one, and present in 3 other sets of plots. The grass-like plants are *Eriophorum, Carex pauciflora, C. dioica, Scheuchzeria,* and *Molinia.* Dicot herbs are *Drosera* and *Melampyrum.* — The ground layer is dominated by *S. recurvum* and *S. medium,* with 6 other moss spp. and (in 2 sets of plots) *Cladonia rangiferina.* — Species-area curves for field layer and moss layer were made for the two sets of data having most species: at Rubskoje the *Cassandra* Association (RC), and at Krupino the *Eriophorum* Association (KE). The moss-layers for both associations at the location near Mironowo (MC and ME) were also studied. The one-piece area estimated to be equivalent to an aggregate of plots (designated I) varies with size and number of plots; where the same number of species accompanies more than one size of equivalent area a compromise value for the area was adopted. Species-numbers used as the basis for five curves are tabulated herewith, as well as species-numbers for moss layer in the other three stands.

Stand	Layer	.247 mlc.	.494 mlc.	3.954 mlc.	I, spp.	I, size in mlc.
RC	Field	5.64	6.63	8.4	17	199
RC	Moss	1.79	2.25	3.0	5	199
KE	Field	4.56	5.95	7.6	13	128
KE	Moss	1.95	2.40	3.4	6	128
MC	Moss	3.22	3.47	4.4	8	213
ME	Moss	2.407	2.582	3.5	5	87
RE	Moss	1.98	2.025	2.1	3	199
KC	Moss	2.281	2.312	2.5	3	88

Results from the curves are unexpected in two ways: for one stand, KE, the reference areas for field layer are considerably smaller than for moss layer (Am values 7.11 and 12.6 mlc.). Location and form of the field-layer S-curve for KE are uncertain, whereas for RC, a regular S-curve exactly fits the four given points. Also, for all five curves, reference areas are much larger than might be expected from earlier determinations of Minimiareal for this and similar types of vegetation in northern Europe. Katz and Katz followed Du Rietz in

using only the field layer for determining Minimiareal; they found no increase in number of constant species from the 4-sq.-m. plot-size to the 16-sq.-m. size, and rightly concluded that the Minimiareal (an area based on adequate content of first-order constants) lies between 1 and 4 sq. m. If any of the reference areas used in the present study might correspond to Minimiareal it is the "smallest representative area," Ar. Yet the lowest Ar value for any of the five raised-bog curves is 5.14 sq. m. (for moss layer in RC). The lowest field-layer Ar (5.75 sq. m. in KE) is perhaps erroneous. The only dependable comparison with the Minimiareal of less than 4 sq. m. is the field-layer Ar for RC, which is 17.5 sq. m. If a smallest representative area based on all species is thus 4 to 7 times as large as that based on first-order constants (those few species which are most numerous and most generally distributed), the contrast between these few and the other species is seen to be highly significant. From at least the statistical viewpoint, Du Rietz's emphasis upon the constant species is amply justified. — Another illustration of the contrast between the generally distributed species and the others (which seems to call for some consideration of the other species also) is the fact that although no new constants are added between 4 and 16 sq. m., yet the increment in total species-number is almost invariably greater between those two areas than in the other four-fold increase from 1 to 4 sq. m. This is true in all ten lines of the foregoing tabulation of species-numbers in the high moors, as applying to absolute value of the species-number increment. Thus in RC field layer, the increment in mean species-number per plot is 0.99 from 1 to 4 sq. m., 1.77 from 4 to 16 sq. m. *Ratios* of increase are likewise greater from 4 to 16 than from 1 to 4, except for the already suspect field layer of KE. For field layer of RC the ratio of increase from 1 to 4 sq. m. is 1.175, from 4 to 16 sq. m. it is 1.267.

When the species-numbers at particular areas are plotted on semi-log paper, the result of the foregoing relations is that the section of the species-area curve which lies between 1 and 16 sq. m. is conspicuously concave, which means, if species-increase continues at accordant rate, that even the smallest reference area, Ar, might be expected to exceed 16 sq. m. Yet for some sets of data in which species-numbers are small, it is questionable whether any section of the curve will yield a two-fold increase in species-number with a fifty-fold increase of area. The further fact that at 1 sq. m. the curve is nearly level makes one suspect that if it were extended into smaller areas, a second steeper section would be found. Unfortunately, data for a range of small areas are not available. In some other bog and dwarf-shrub communities and in chaparral there have been earlier suggestions that their species-area curves are double curves: that the few first-order constants have attained a nearly level upper section at one or a few square meters, at which size other species are at the bottom of their curve. Field investigation into this possibility should embrace a series of replicated one-piece areas, in steps representing about a four-fold increase in extent, and ranging (in bogs) from $\frac{1}{256}$ or $\frac{1}{64}$ sq. m. to perhaps 1024 sq. m. The preparation of

curves from so dependable a series of areas in fine-textured communities of few species should decide incidentally whether in some communities no part of the curve will yield twice as many species with fifty times the extent, and if so suggest criteria for sufficiency of area in such communities.

ARTEMISIA CANA BUSH, WITH BOUTELOUA–AGROPYRON–STIPA. WESTERN NORTH DAKOTA. HANSON AND WHITMAN (1938: 61, 75). The authors' Test Area 18, representing their Type 5, is one of three examples in which *A. cana* is the dominant bush. Area 18 is well grassed. The site is a low terrace above Garner Creek on Olstad Ranch, 16 miles s. e. of Sentinel Butte. Soil is brown clay, without excess of solutes, and with subsoil moisture available at all times. *A. cana* is in certain respects, such as stature, habit, and spacing, similar to *A. tridentata* of farther west. *B. gracilis, A. Smithii,* and *S. viridula* are the only notable species of the grassland phase. (*S. viridula* is common at borders of thickets at the front of the Rocky Mountains; it is significant in only this one of Hanson and Whitman's 10 types).

From statement of size of bushes, and from data in Hanson and Whitman's Table 1 on relative importance of species, supplemented by random spotting of bushes on a hypothetical map including 15 plots, the following approximate figures were inferred. The average bush covers 10 sq. ft. within an area of 36.7 sq. ft. Bushes per acre, 1187. Percentage of area occupied by bushes, 27.3. Presumed frequency of bushes, 60% (in 18 of 30 separated 1-sq.-m. plots). Stated av. no. of spp. per plot 12.9; 40 spp. in the 30 plots. One-piece equivalent area (to include the 40 spp.), 11.76 mlc. From these figures it was possible to construct a curve for this two-phase mixture, with results as in Table 24 (minimum area 10.8 mlc.).

THE BUSH PHASE. It is impossible to apply to a one-species community or vegetation-component the same criterion for sufficiency of area that is used for a unit with numerous species. An approach can perhaps be made by considering a characteristic that is usually definable: spacing. If spacing is nearly uniform, as it frequently is in xeric bush or shrub, or in many stands of juniper or of pinyon in western North America, one can determine the area required to include a certain minimum number of individual plants of the species. It will be necessary for many students of vegetation to reach agreement on the value of this minimum number. Theoretically, the smallest area which will almost surely contain one individual of representative size or age, is big enough, if one knows that other sample areas of the same size will contain the same species and no others. The smaller the arbitrarily-adopted minimum number, the greater will be the variability as among sample-plots in one stand, or as between different stands. To reduce variability, particularly if one is studying stands that are far from uniform in spacing, a number no smaller than 10 is suggested for field trials. In the other direction, it has been found that the number of individuals in Am or minimum area for a mixed community with many species ranges from

504 down to 100 or fewer. The figure 504 was found for trees 3″ + in 4 acres of mixed deciduous forest (Brownfield Woods: see Vestal and Heermans, 1945: 131, "number of trees as a criterion of plot size"). In this forest the marked numerical preponderance of one species makes the number of trees in the minimum area several times that of a more nearly equable mixture. In comparing mixed types with one-species types, there is reason to believe that the reference area Ar or "smallest representative area," only one-fifth the size of Am or minimum area, is more nearly comparable to the size adequate for a single-species type. If this is true, 101 trees for Brownfield, 20 to 25 trees as a minimum for a simpler or equable mixture, and perhaps fewer than 10 for a pure stand, are equivalent in determining the sizes that are adequate in degree of information provided by one sample plot.

Here may be interjected a recommendation for various types of silvicultural research, from a publication by Munns and others (1935:9): "As a general rule, a plot should be of such size that at the end of the experiment it will contain at least 100 trees of the predominating age-class."

The foregoing statements apply only to types dominated by woody species in which individuals are readily distinguished. For some grass-dominated types, and for certain herb ground-covers in forest, other characteristics or criteria need attention.

To deal specifically with *Artemisia cana* bush, spacing is close in Test Area 19 of Hanson and Whitman, fairly close in No. 20, rather open in No. 18, the one here treated. The likely plot-size to contain 10 bushes in each of the three stands would approximate these values (in the same order): 3.2, 3.9, and 8.4 milacres, or 13.0, 15.8, and 34.1 sq. m. The smallest plot almost sure to contain one bush is (in Test Area 18) about 2.1 milacre, or 8.5 sq. m.

The grass phase. Two views are possible of species-area characteristics of the grassland part of the combination. According to the first view, one regards the grass cover as it is, merely subtracting one species (*A. cana*) from the S-value at any area large enough to include at least one bush. Species-number for 1 sq. m. is reduced by an insignificant amount, from 12.9 to 12.3. A species-area curve would lie just below that for the bush–grass complex: the reference areas would be larger by a trivial amount. The other view is hypothetical, considering the size of reference areas if the bushes were not present, and the grass cover occupied all the area of the terrace. Aside from minor differences in composition, which presumably would make slight or no difference in total number of species, the effect would be to reduce the area required for a particular S-value, in the proportion of space occupied by the bushes, 27.3 per cent. Thus, in place of 12.9 spp. at .247 mlc. and 50 spp. at 11.76 mlc. *with A. cana,* we have 12.3 spp. at .18 mlc. and 49 spp. at 8.55 mlc. without *A. cana.* The curve is displaced to the left, making reference areas significantly smaller: Am is reduced from 10.8 to 8.48 mlc. This effect would be greater in other sagebrush–grass stands if the bushes occupied larger proportions of the total area. Since actual

increases or decreases in the bush part of such dual communities are very common in the West, and since the same relations are found in pastures invaded by shrubs or junipers, or by hawthorn or other weed-trees, or by bushy clumps of cacti, they are of more than hypothetical interest. Reference areas are smaller in inverse proportion to space occupied by the fine-textured phase.

Short-grass–bush mixture, east of Boulder, Colorado. Vestal (1914: 398). This weedy grassland with suffrutices was called the undershrub formation by Pound and Clements, the *Gutierrezia–Artemisia* association by Shantz. It may replace short-grass and other plains grasslands as a consequence of grazing. The particular area studied is a rocky terrace-remnant 4 miles east of Boulder. Its north end was covered with weedy grass cover with many small bushes of *Artemisia frigida,* commonly considered a herb, and *Eriogonum effusum.* (A photograph of this vegetation is shown as Fig. 9 in the article cited). *Gutierrezia* was much less common, but was the conspicuous dominant in the larger area south of a fence which enclosed the north end. The north part had not been grazed in the period just preceding the time of study (Sept. 1913). Other perennials of growth-form other than herbs were *Opuntia polyacantha* and *Yucca glauca.* Estimated density of bushes is 8800 per acre. Four grasses, *Bouteloua gracilis, Agropyron Smithii, Sitanion brevifolium,* and *Stipa comata,* covered 35% of the surface, but much of this cover seemed dead. Conspicuous herbs were *Psoralea tenuiflora, Artemisia canadensis, Chrysopsis, Grindelia, Sphaeralcea, Lithospermum, Boebera,* etc. — A general census of the north part was supplemented by details in 5 1-sq.-m. quadrats, separated. Analysis of data gave species-numbers for bushlets and for herbs in six plot-sizes. Treatment of this mixture differs from the preceding (*A. cana* plus grass) in two respects: there are enough "woody" species to serve for a species-area curve for the bush phase; and the grass phase is treated as it is, not as it would be if bushes were absent.

A result of this treatment of the grass phase is that its Am value (8.13 mlc.) is higher than that for the combination (7.14 mlc.). The composite curve is a simple summation of curves for the two phases.

Bush–short-grass mixture, San Luis Valley, Southern Colorado. Ramaley (1942: 260-263, Tables 5-7). The bush part has been briefly mentioned earlier under the name *Chrysothamnus–Gutierrezia* bush. The whole mixture is xeric and open, with usually somewhat more than half the surface bare. Ramaley gives three tabulations, one for 3 1-sq.-m. quadrats near Villa Grove at the north end of this large intermont plain, one for 50 0.1sq.-m. plots in San Luis Hills (south end), one for 4 4-sq.-m. quadrats on black lava west of Capulin (southwest border of the valley). In the Villa Grove plots, a ground microphyte, the lichen *Parmelia molliuscula,* covers 13% of surface.

The Chrysothamnus–Gutierrezia bush phase. Three bush species lead in both Villa Grove (VG) plots and in San Luis Hills (SL) plots. They

are *Chrysothamnus* sp., *Gutierrezia diversifolia,* and *Opuntia polyacantha* (included with the bushes). *Artemisia frigida,* here a low bush, is in 2 of the 3 VG plots. Only *Chrysothamnus* occurs in the Capulin plots. In extensive areas of this community, most of the following species are found: 1 or 2 large-growing *Chrysothamnus* species, less frequent than low *Chrysothamnus* bushes of 2 to 5 species; *Gutierrezia; Artemisia frigida, Yucca glauca, Senecio spartioides,* 1 or 2 small-bush species of *Eriogonum, Eurotia lanata, Atriplex canescens.* Bushes cover 15 to 25% of the ground. The estimate for ground-space per bush is 0.214 milacre, with 4673 bushes per acre. Data are hardly sufficient for a species-area curve, but one was tentatively drawn from a small-area point, 0.6 spp. at 0.128 mlc., nearly parallel to the curve for sagebrush (the neighboring and similar community of San Luis Valley, with mostly the same bush spp.) This tentative curve gives Am value 27 mlc., Sm 5.73 spp., as compared with 44.7 and 5.30 for sagebrush, which has larger bushes.

The short-grass phase. Blue grama grass, *Bouteloua gracilis,* is the only leading species in all three of Ramaley's localities. Herbs are so few in the SL plots that these plots are not used in this species-area treatment. The grass phase is much the same as short-grass of the Great Plains. The number of grass and herb species is considerable (Ramaley lists about 56), but one might need to examine 5 to 10 square miles to encounter so many. In any one locality, species are relatively few. Some of the more frequent species are: *Muhlenbergia Torreyi, Stipa comata, Sporobolus* sp., *Sphaeralcea coccinea, Hymenoxys floribunda,* and *Senecio Fendleri.* Locally frequent are species of *Carex, Comandra, Eriogonum, Potentilla, Astragalus, Lupinus, Gilia, Oreocarya, Chrysopsis, Grindelia.* — The VG plots are considered normal for the type; in them herbs cover about 22.3 sq. decimeters per 1-sq.-m. plot. In the lava near Capulin (LC plots), there is practically no soil; plants grow in crevices, and herbs cover only 41 sq. dm. per 4-sq.-m. plot. The effective size of LC plots is thus nearer 2 sq. m. than 4. Species-numbers are thus available for 2 small plot-sizes, and for aggregates of 2, 3, and 4 plots. Average no. of spp. per 1-sq.-m. plot (VG) is 4.0; per 2-sq.-m. plot (LC) is 3.25. Herb spp. in the 3 VG plots: 5, of which 3 are grasses. Herb spp. in 4 LC plots: 7, including 4 grasses. One-piece areas equivalent to the aggregates ranged from 0.618 milacres for 2 1-sq.-m. plots to 3.56 mlc. for 4 2-sq.-m. plots. For larger areas, 18 species are estimated to require 21 mlc.; 35 spp. to require 800 mlc. — The reference areas found from the curve are very large (Am is 125.5 mlc.). This may be explained by the large amount of bare surface (usually 50% or somewhat more), by occurrence of bushes in the same area, and by the poor representation in both individuals and species of grassland plants other than *Bouteloua.* It is notable that in this mixture the minimum area for bushes, 27 mlc., is much smaller than that for the herbs.

Chrysothamnus–Gutierrezia plus short-grass. As in the example of short-grass plus small bushes on the stony terrace east of Boulder, a composite curve for this bush–grass combination of San Luis Valley may not be with-

out meaning. Simple addition of grass and bush species-numbers at particular areas gives a basis for the composite curve. The resulting Am value, 100.8 mlc., is considerably smaller than that for grass alone.

Bush–grass garigue: Erica multiflora formation, southern France. C. Raunkiaer (1916:234, Table 3). The bush phase of this mixture was included with other Mediterranean shrub types in Table 9. Raunkiaer listed in 50 0.1-sq.-m. plots 8 low-shrub spp. and 34 others. Of these 34, 10 are regarded as bushes, 24 as herbs. Considering all woody species as comprising the bush phase, their occurrences in plots total 202, making 4.04 species per plot. Grasses and herbs have 141 occurrences, thus 2.82 spp. per plot. The most frequent shrub or bush spp. are *Erica multiflora* and *Fumana procumbens,* each in 34 plots, *Thymus vulgaris* in 25, *Rosmarinus officinalis* in 23, *Helianthemum polifolium* 19, *Genista scorpius* 14. In spaces between bushes are the grasses and herbs. Occurrences for the six most frequent of these are: *Festuca ovina* 28, *Trinia dioica* 12, *Aphyllanthes monspeliensis* 11, *Stipa juncea* 10, *Hieracium pictum* 9, *Asperula cynanchica* 8. Lower scores for these than for woody species result not only from their subordinate status in the complex, but also from Raunkiaer's method of counting all those plants whose crowns overlap the plot. Effective plot-size is thus larger for the larger plants. It is estimated as 0.7 sq. m. for bushes, and 0.2 sq. m. for herbs. The one-piece area equivalent to the aggregate is also separately estimated for the two phases: 14.96 mlc. for bushes, 5.44 mlc. for herbs. Two points can be plotted for the curve of each of the two phases: the curve drawn for grass is regularly higher than that for bush. Ratio of species-number varies little from small to large areas. — Species-numbers for the composite curve were obtained at six areas by simply adding S-values read from grass and bush curves at those areas.

Creosote-bush desert, Coachella Valley, California, and Gila Valley, Arizona. H. L. Shantz and R. L. Piemeisel (1924: 733-745). *Covillea glutinosa,* now usually called *Larrea divaricata,* is the dominant shrub of this most extensive type. It is the usual vegetation on well-drained desert surfaces, especially rocky outwash slopes or bajadas. The authors studied it in Coachella Valley north of Salton Sea, and near Chandler, Arizona, between Gila River and its tributary, Salt River. The only common woody associate of *Larrea* in these districts is *Franseria dumosa,* a bush ragweed with bur fruits. One shrub (*Krameria Grayi*) and 7 bush species are the other woody plants of the type in Coachella Valley (CV); one shrub (*Zizyphus* or *Condalia lycioides*), and 1 bush (a *Lycium*) are the others in Gila Valley (GV). Herb cover consists mostly of spring annuals; it varies greatly in density and in composition from spot to spot and from year to year. Common species are *Plantago erecta, Baeria chrysostoma, Pectocarya penicillata, Amsinckia Menziesii,* and *Thelypodium lasiophyllum.* The lists of common or frequent herbs include 23 spp. for CV and 20 for GV. Of less frequent or rare herbs, 35 are given for CV, 21 for GV.

The two 100-sq.-m. quadrat-maps shown for woody plants include only one species, *Larrea*. A map of the herbs in 1 sq. m. is shown from near Chandler, recorded in late March, 1915. It includes 11 herb species. It is presumed that the same area may later have had a few more species (after the summer rains). In CV this would not be likely. — Plot-map analysis was used to find species-numbers for small areas; these data were supplemented by very rough approximations for large areas. Sample figures, some of which were read from the species-area curves, are as follows:

Creosote-bush: Species-Numbers at Certain Areas.

		.0618 *mlc.*	.247 *mlc.*	10 *mlc.*	100 *mlc.*	1000 *mlc.*
Woody species:	CV	——	——	0.56	2.18	4.67
	GV	——	——	0.73	1.56	2.55
Herb species:	CV	11.1	16	33.2	42.1	49.0
	GV	10.1	14	30.0	38.0	43.8

In reviewing reference-area findings, the Am values for woody species are very large (530 and 1908 mlc.) as compared with other examples of shrubby vegetation. This is attributed to the open spacing, as well as to the relatively great scarcity of individual bushes of species other than *Larrea* and *Franseria*. The difference between California and Arizona desert shrub examples is pronounced. The S-curve for GV has a feeble gradient (only 4 woody species are listed for the vicinity of Chandler), and its rate of species-increase falls off much more rapidly than that of the CV curve.

The statements of Forrest Shreve (1942: 205-207) as to minimal areas in desert vegetation-types are of interest here: In nearly pure stands minimal area is determined by the spacing. In mixed stands [probably much denser than these creosote-bush examples] the minimal area is often not more than 100 sq. m. In rich stands the minimal area must be enlarged to a 500-meter square.

As to the herb populations of the desert floor in CV and GV, their Am values are comparable to those of fine-textured grasslands. The ground-space in few places is so fully occupied that any of the species are excluded by competition of other species from an area larger than a few square feet.

Additional mixtures. In addition to the conspicuously heterogeneous examples of vegetation just examined, some of the others for which only one curve was prepared may deserve further study, with separate curves for different layers, phases, or components. Almost any stratified forest, and the sclerophyll oak woodland, which shows marked discontinuity (true of many open woody types properly called woodland rather than forest), thus qualify as complexes. The *Sideroxylon* thicket is three-storied. The *Philippia* heath has semi-open top layer of shrubs, with lower ground-cover of several unlike growth-forms. Certain Mediterranean shrub and bush types should be studied in the field as complexes. They represent many combinations of unlike growth-forms. The same

is true of heaths, particularly those with tall-shrub dominants. In heaths, open forests, and in bogs, dwarf-shrub dominants are intermingled with grasses, herbs, and microphytes in innumerable combinations. The *Vaccinium–Dryas* heath with herbs (on Mt. Njulja) is a good example, less complex than some others. The generally complex composition of grasslands is not sufficiently realized: Regel's emphasis upon inequalities of make-up of his *Festuca rubra* meadows is similar to Jaccard's pointing-out of conspicuous differences in "composition florale élémentaire." Most prairies are patchworks or mosaics of diverse elements. However, to the extent that they are not too greatly different in stature and bulk, these unlike elements may be treated together in species-area studies. As grasslands extend into semi-arid countries, suffrutescent herbs and low bushes become more numerous, and may require separate examination as a bush phase. Another growth-form in some tropical grasslands is that with greatly thickened underground woody stem or xylopodium. This may be one of the dominant growth-forms over great expanses, as in Portuguese West Africa, but plants with xylopodia or xylorhizae are commonly an element in mixed tropical grasslands.

Among the elements of bogs here studied, one or another form of *Oxycoccus* (cranberry) mingles freely with sedges where other dwarf-shrub elements are absent. The *Chamaedaphne* bog reported by Kenoyer appears to be notably heterogeneous. The communities developing on rocky surfaces seem to be accidental assemblages of elements from diverse sources. Some of these communities might be like the Boulder mesa-top in requiring separate treatment for unlike parts. Even the lichen communities may be heterogeneous, as in the Howenstine talus, with rock *Cladonias* and also smaller *Cladonias* on fallen logs and branches.

In the author's opinion, frank recognition of the diversity of composition of most communities is desirable. More and more students of vegetation are willing to concede the fact of diversity and the reality of the units of composition, whether these are called synusiae, components, elements, constituents, or something else. A fairly recent tendency in Europe to suppress the term synusia, and to use instead the term society, seems to the writer to be a backward step. Society (as used in Britain and America) is more like the term facies, and is applied mainly to species other than the dominants. To say that a unit of composition should be called by a name that emphasizes an *appearance* (because of local or temporary conspicuousness of one or several species) is indefensible. It not only quite unnecessarily obscures an important characteristic (that the synusia is a unit of *composition*) but it spoils the term society, which should continue to mean a group or layer or seasonal aspect of a community, usually conspicuous in its appearance.

ANIMAL COMMUNITIES AND ASSEMBLAGES

By animal assemblage is meant a part of a community, such as nesting birds within a forest. Results for a very few groupings of animals which have been

studied suggest that their species-area relations are amenable to methods used for vegetation. The species-area curves seem to be of S-form, and reference areas may be found in the same manner. Results from the first two examples are:

	Am	Sr	Sm	D
Sea-bottom fauna, Thisted Bredning, Jutland	3.32 sq. m.	10.0	14.35	2
Apterygota, oak-forest mold, Switzerland	101.7 sq. cm.	9.65	14.6	2

Sea-bottom, Thisted Bredning in Limfjord. C. H. Joh. Petersen and P. Boysen Jensen (1911, Table 1). In this classic study, "The Valuation of the Sea," the two authors reported results with a bottom sampler from different bodies of sea water. Limfjord is the branching passage with alternate straits and *brednings* which crosses northern Jutland. Thisted Bredning is about 21 km. long, 4 to 7 km. wide, and in most parts 10 or 11 meters deep. Its shallow margin has a well-developed zone of *Zostera.* In October of 1909, and April and October of 1910, the bottom was sampled at 100 stations: the animal populations are larger during spring. Table 1, summarizing the first set of 100 samples, was used for a species-area curve. The sampler used in 1909 took in material from 1346 sq. cm. of bottom (0.0333 mlc.). The 3 sets include 35 spp. or closely-similar groups of two or several species. Table 1 includes 25 spp. or groups. The most abundant species are *Ophioglypha* sp. (a brittle-star); the lamellibranchs *Pectinaria belgica, Nucula nitida, Solen pellucidus, Mya truncata;* the gastropod *Philine aperta;* nereids, etc. Though the basis for estimating one-piece areas equivalent to plot-aggregates was slight, species-numbers were found for aggregates of 2, 4, 10, and 25 plots. For two sizes smaller than 1 plot, random spotting on a map of 4 plots gave likely species-numbers. Some of the species-numbers and one-piece areas used for plotting are:

Area, mlc.	.0037	.0333	.439	1.546	4.85	25.0
Species	2.65	6.85	11.0	14.33	16.5	25.0

The fit of curve to points is not very good. The Am value 3.32 sq. m., or 0.821 milacres, is about that of a fine-textured grassland (e.g., Daubenmire's *Agropyron–Poa secunda* type in Garfield Co., Washington: Am is 0.779 mlc.).

Apterygota from forest soil, Aire-la-Ville, Kanton Genf. H. Gisin (1945). The "plot-size" for study of these small arthropods was 70 sq. cm., since samples of that extent were removed from the surface soil. (The depth was ca. 5 cm., volume of sample ⅓ liter.) Samples were from 4 localities separated by intervals of ca. 5 meters, with 3 samples from each of the first 2 localities, 1 each from the others. Gisin summarizes his findings in a table, which excludes 5 spp. (some young individuals and a large *Tomocerus,* incompletely known). The table shows for each of 17 species its occurrence in the respective samples, and also its degree of abundance. Gisin decided that over half of the species are *sehr stetig* (8 of them occur in all 8 samples, and 1 occurs in 7). The most abundant species are *Folsomia quadrioculata, Pseudosinella duodecimpunctata,*

Onychiurus armatus, and *Isotomiella minor*. Since the average ⅓-liter sample yielded 78% of all the species found in the 8 samples, Gisin concluded that the *Minimalraum* is not far from the one-sample size. — To prepare an S-curve, mean numbers of species for 1 plot, for 2 neighboring plots, and for 3 neighboring plots were found. If these means are slightly reduced to correct for the somewhat smaller number of species in locality 3, we find that the average for 1 plot is 13.50, for 2 plots 15.46, for 3 plots 16.69. Using Gisin's total of 18 species for 8 plots, we have 4 points, which prove to be all on the convex section of the curve. However it seems clear that the Am value is in the same order of size as Gisin's Minimalraum. His is 70 sq. cm.; from the curve it is 101.7. Gisin considers it essential to study numerous samples of Minimalraum size.

Stream fishes, Champaign county, Illinois. D. H. Thompson and F. D. Hunt (1930). The authors emphasize area relations in several ways. Since habitat-complexes vary with size of stream, ten classes are distinguished in a geometric series according to area of the drainage basin above the point of collection. Drainage area, being constant, is a more convenient criterion than volume of flow. The ten area-classes are: 0.5-1 square miles, 1-2, 2-4 . . . 256-512. Tables 1 to 7 show for particular groups of fishes how a progressive increase in number of species accompanies increase in stream size. (A smoothed graph was made showing number of species of all groups plotted against logarithm of area: it has the S-form, but is not comparable to the usual species-area curve.) — The authors had so designed the field study that larger areas of stream were seined in the places representing larger area-classes; number and extent of collection-areas, and consequently also the extent of aggregate collection-areas, were separately recorded for each of the ten size-classes. This is like choosing a graduated series of plot-sizes for work with land vegetation, and makes it possible to apply similar species-area treatment to the data. Figures on p. 15 of the article by Thompson and Hunt show for each drainage-area class the number of collections, the area per collection (in square yards), and the total area seined. The total number of species collected in each drainage-area class had been found from Tables 1 to 7. These totals vary from 10 species from stream-points of smallest area-class to 54 species in the ninth area-class (128-256 sq. miles). Class 7 has 46 spp; class 10 has 42 spp. The entire list from all area-classes numbers 70 spp. — Mean numbers of species per collection were found from the interesting graph by Thompson and Hunt, their Fig. 6, p. 42. It was also necessary to estimate the one-piece area which is equivalent in no. of spp. to each aggregate of well-separated collections (the total collection area). When this was done, species-area curves could be made. (Each is based on only two points, and is thus of low dependability.) — It seemed that results could be of more general import if data for successive drainage-area classes were first smoothed. This was done graphically. Smoothed data for 5 of the 10 classes are tabulated here, with collection areas converted to milacres.

Drainage area *sq. miles*		Av. area per coll., *mlc.*	Av. no. of spp. per coll.	Total coll. area, *mlc.*	1-piece equiv. area, *mlc.*	Total no. of spp.
1.5	(1-2)	6.28	4.6	60	436	13.6
6	(4-8)	10.2	8.3	148	1078	26.6
24	(16-32)	15.3	12.0	236	1740	36.7
96	(64-128)	19.9	14.7	290	2139	43.0
384	(256-512)	23.0	16.6	333	2450	47.6

Champaign county does not have large enough streams to show whether collection points with drainage areas exceeding 512 square miles would continue to yield progressively greater numbers of species. In the following table of results from the five species-area curves drawn, Am-values are in milacres and square meters as in previous tables; also in square yards, to permit direct comparison with collection areas as given by Thompson and Hunt. All curves and results have Dependability 3.

TABLE 25. Stream Fishes, Champaign County, Illinois.

Drainage area, *sq. miles*		Am, *mlc.*	Am, *sq. m.*	Am, *sq. yds*	Sr	Sm
1.5	(1-2)	75.0	303.4	363	7.17	10.7
6	(4-8)	168.5	682	815	13.9	20.5
24	(16-32)	242.5	981	1172	19.0	28.0
96	(64-128)	310	1254	1500	22.4	32.8
384	(256-512)	318	1286	1538	24.4	35.8

Since collections are from different streams, and habitats are not usually homogeneous at one collecting point, each line of the table represents a composite of fish assemblages. Because different streams have their faunistic peculiarities, species-numbers in the table are higher than will be found in a given stream at any one station.

It remains to consider possible application of Am values to future stream samplings. Present field methods cannot usually reveal the number of species in a predetermined area of stream so large as the minimum areas given in the table. One can, however, with greater economy of effort utilize the seining method of Thompson and Hunt. One can use known or tentative Am values in estimating how many collections to make in nearby and similar parts of a given station, and how large the collection-area should be. Thus for a station of 6-sq.-mile drainage area, one might require the number of species in an Am of 815 sq. yards. The smoothed value of the area per collection for this stream-size had been found to be 49.4 sq. yds. If this were a plot in land vegetation, 6 such plots somewhat separated (say by 6 plot-diameters) would be equivalent to a one-piece area of 919 sq. yards. (The area-multiplier for this number of plots and interval of separation has been tentatively found to be ca. 3.1. 3.1 $\times$ the aggregate area, which is 6 $\times$ 49.4, equals 919.) Since this is larger than required, the collection-area can be reduced in the ratio 815 : 919, making it 43.8 sq. yards. For this and four other stream sizes the figures are tabulated herewith. The multi-

plier for 5 somewhat separated plots is 3.05. Areas (except those of drainage basins) are in square yards.

Am, Converted to Number and Size of Collection-Areas.

Drainage area sq. miles	Required Am	Trial coll.-area	Collections required	One-piece equiv. area	Adjusted coll.-area
1.5	363	30.4	5	463.8	23.8
6	815	49.4	6	919	43.8
24	1172	73.8	6	1373	63.0
96	1500	96.2	6	1789	80.7
384	1538	111.5	5	1700	101

REVIEW OF SPECIES-AREA FINDINGS

MAGNITUDE AND RANGE OF REFERENCE AREAS FOR DIFFERENT TYPES

The principal numerical results from species-area curves for various communities, already shown in Tables 2 to 24, can be viewed together in Table 26, which combines similar communities into groups. For each group, mean value and also the size-range of minimum areas are shown. A few examples which lie outside what seems to be the ordinary range of sizes are omitted, as well as some others with very uncertain values, such as the Pernambuco and Lagoa Santa forests. Five types are each represented by a single example; 11 groups by fewer than 5 examples. Most of the grasslands are included in groups made up as nearly as possible according to vegetational and geographic similarity. The Buena Vista example was put with plains and mountain-border rather than with mountain types. European and west-American mountain grasslands were put together, leaving European lowland prairies and meadows as a separate group. The grasslands were also segregated arbitrarily into five size-groups according to mean value of minimum area. Two sand-prairie examples with Am >45 were omitted. Readers should have no difficulty identifying most groups with the respective series or parts of series of types shown in Tables 2 to 24, except tropical forests, in which similar types were put together from different parts of the world. The mixed rain forests were put in two groups for which the basis of differentiation (quality of stand and site) is inadequately known. If these 24 examples are combined in one group, its mean Am is 7935 mlc; mean Sm is 86.4; mean N1000 is 179.4.

An even simpler view of the gamut of sizes for vegetation-units is provided in Fig. 5, which shows graphically some of the groups of Table 26. This is supplemented by the selection of representative species-area curves shown together in Fig. 6.

TABLE 26. Summary of Means and Ranges of Minimum Areas for Particular Groups of Communities.*

No.	Description of group	N	Mean Am	Am range	Mean Sm	Density
1	Lichen communities	6	0.10	0.0235– 0.14	12.9	
2	"Most compact" grasslands	7	1.44	0.70– 1.99	21.2	*?40 000*
3	"Medium compact" grasslands	13	3.59	2.00– 4.99	37.1	*?10 000*
4	Columbia Basin prairies	6	4.59	0.77– 12.6	24.9	
5	European grasslands, excl. mts.	9	5.34	1.63– 15.1	42.9	
6	Dwarf-shrub in bogs	5	6.62	0.77– 21.6	10.6	
7	Mountain grasslands	13	6.68	1.74– 16.5	45.8	
8	"Medium coarse" grasslands	12	6.79	5.00– 8.99	44.1	*?2 200*
9	Plains & mt.-border grasslands	8	7.21	1.10– 16.2	27.8	
10	Mediterranean bush types	3	?7.78	6.65– 10.0	?10.2	
11	Moss-layer of bogs	4	8.61	5.00– 12.6	6.99	
12	Grasslands in general	55	9.93	?0.70– 44.9	38.7	
13	Prairies, interior N. Am.	7	10.4	6.30– 17.9	57.4	*(2 022)*
14	Mediterranean shrub types	4	?12.2	6.50– 27.7	?9.12	
15	"Coarse" grasslands	15	13.3	9.00– 17.9	46.7	*?1 250*
16	*Vaccinium—Dryas*—herbs	1	14.9	–	27.9	
17	Sand prairies	7	19.4	13.00– 44.3	31.1	*(103)*
18	Sedge bogs (field-layer)	5	22.3	1.16– 100	13.3	
19	"Open, sparse" grasslands	8	26.0	18.00– 44.9	33.8	*?250*
20	Bush types, Colorado	5	27.9	2.77– 46.0	4.38	3 985
21	Dwarf-shrub heaths	7	43.1	21.3 – 103.2	13.9	
22	Bracken-Blueberry	8	58.3	47.7 – 73.7	40.2	
23	Herb ground-cover in forest	8	67.8	43.1 – 81.7	29.7	
24	Dwarf-shrub g.-c. in forest	7	71.0	49.0 – 107	21.3	
25	*Sideroxylon* thicket	1	92.4	–	69.0	15 520
26	California bush types	2	135	134– 136	12.0	?5 510
27	*Philippia* heath	1	164	–	28.0	8 920
28	Shrubs in forest	2	169	143– 195	8.2	
29	Chaparral types	8	186	56– 450	18.0	(3 215)
30	Oak woodland, sclerophyll	1	319	–	8.7	
31	Mt. forests, low-latitude	3	511	280– 764	18.3	561
32	Young conifer forest	1	519	–	12.1	
33	Ground vegetation under teak	7	707	484– 910	57.3	
34	Old-growth pine forests	2	769	678– 860	8.7	314
35	Less-mixed deciduous forests	6	1 092	718– 1 800	9.0	314
36	Desert shrub *(Larrea)*	2	1 219	530– 1 908	2.6	
37	Mixed deciduous forests	19	2 185	868– 4 015	16.9	192
38	Subtropical & mid-mt. forests	3	2 291	1 575– 3 441	64.6	612
39	Tropical secondary forests	5	3 926	1 320– 5 585	112.8	318
40	Tropical mixed r. f., good	16	6 753	3 890–11 550	91.2	189
41	Heath forests, trop. lowlands	3	7 603	6 265–10 000	82.7	216
42	Tropical mixed r. f., fair	8	10 297	5 592–19 500	76.7	160
43	Tropical river or swamp forests	2	16 183	10 715–21 650	75.4	154

* Minimum areas (Am-values) are in milacres (1 mlc.=4.04687 sq. m.). Sm is the number of species at minimum area. See text for statement of communities or stands excluded. Groups are in order of mean Am-values. N is the number of examples in each group. Densities for certain grasslands, in italic figures, are numbers of plants per milacre; for certain shrub types or forests, ordinary figures represent numbers per acre. The diameter-limit for trees is 3 inches. A number in parentheses is not the mean density for a group, but is based on only 1 to 4 examples. Densities for the five grassland size-groups are very rough estimates.

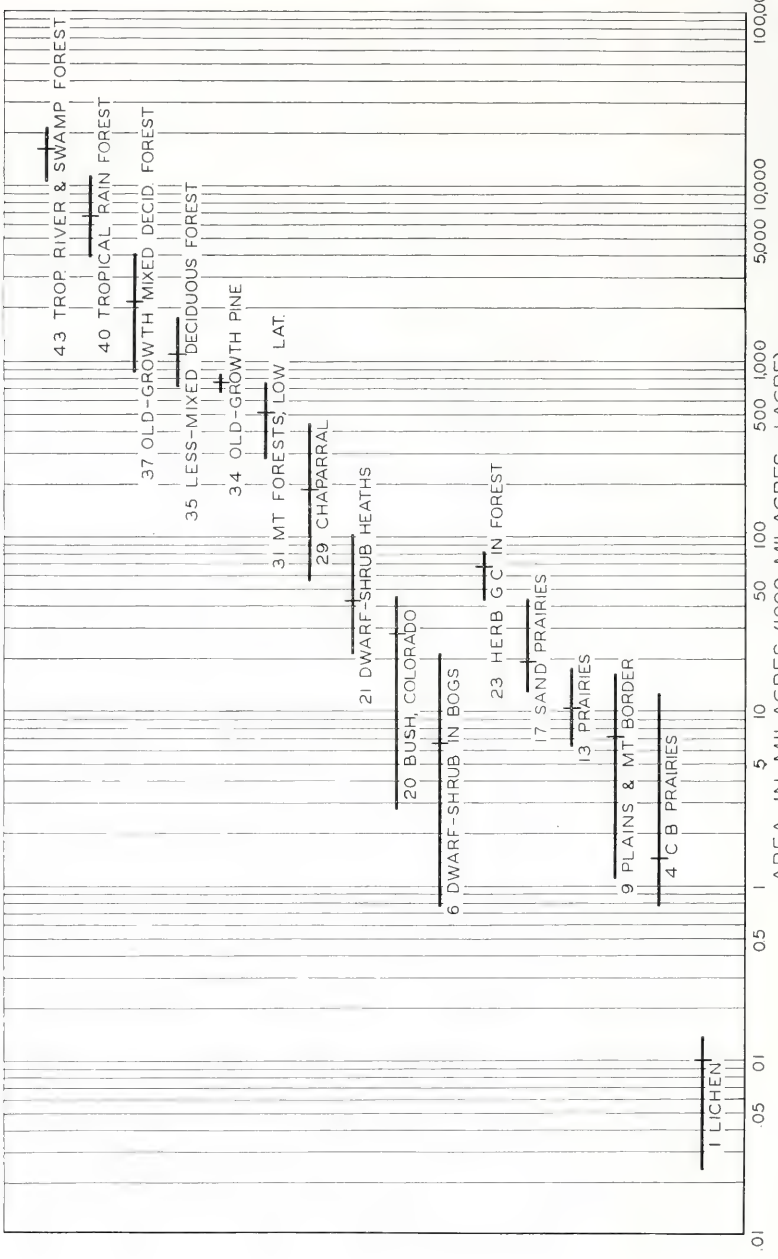
43 TROP. RIVER & SWAMP FOREST
40 TROPICAL RAIN FOREST
37 OLD-GROWTH MIXED DECID FOREST
35 LESS-MIXED DECIDUOUS FOREST
34 OLD-GROWTH PINE
31 MT FORESTS, LOW LAT
29 CHAPARRAL
21 DWARF-SHRUB HEATHS
20 BUSH, COLORADO
6 DWARF-SHRUB IN BOGS
23 HERB G C IN FOREST
17 SAND PRAIRIES
13 PRAIRIES
9 PLAINS & MT BORDER
4 C B PRAIRIES
1 LICHEN
.01 .05 .01 .05 1 5 10 50 100 500 1,000 5,000 10,000 100,000
AREA IN MILACRES (1000 MILACRES = 1 ACRE)

FIGURE 5. Graphic representation of ranges of minimum areas for groups of communities selected from Table 26. Positions of mean minimum areas (mean Am values) are also shown. Numbering of groups is the same as in the table, which shows numerically these same size-ranges and means. Microphyte and herbaceous communities are near the bottom of this figure; bush and shrub vegetations in the middle; forests above and to the right.

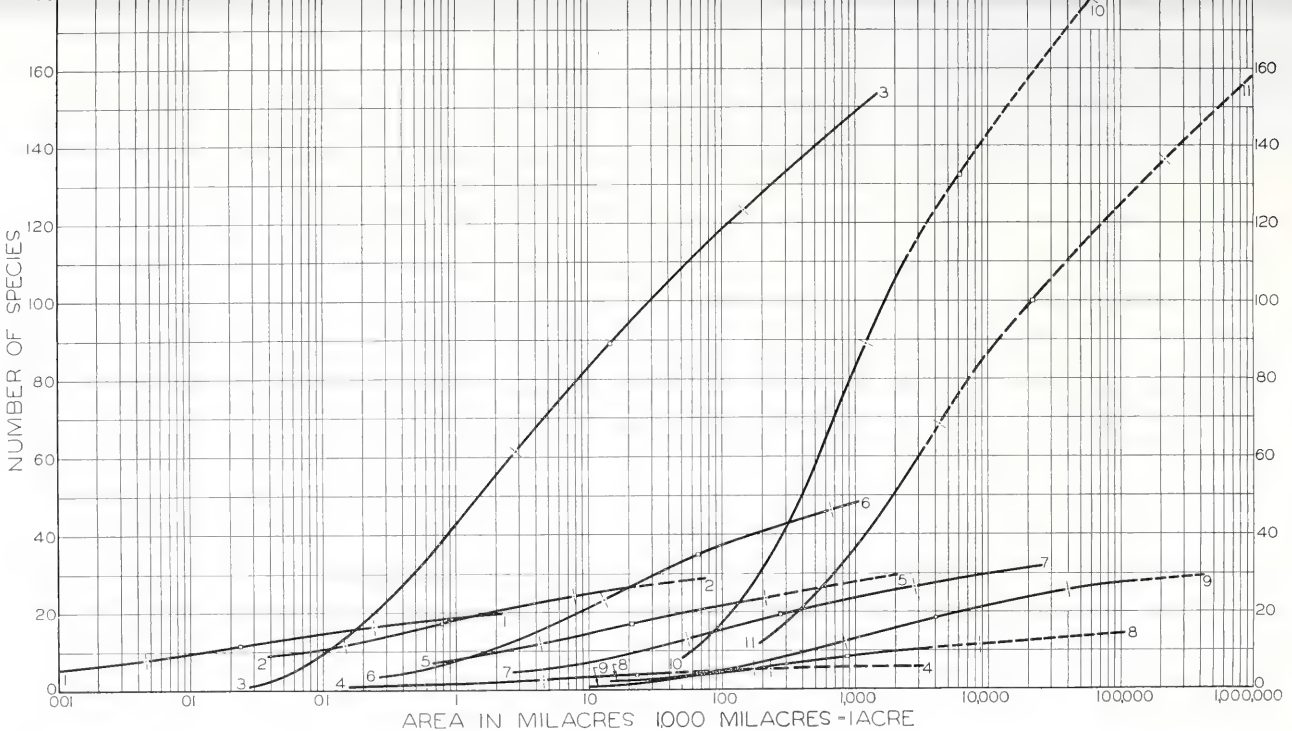

FIGURE 6. A procession of species-area curves for eleven communities. All are drawn to the same scales. The curves for all but three floristically rich communities are thereby much flattened as compared with the original curves, each drawn to a vertical scale appropriate to its own number of species. Further information on the communities represented by the numbered curves will be found in the preceding section.

No.	Description	Am, *mlc.*	Sm
1	*Lecanora deusta* association of smallest lichens	0.0235	11.7
2	Compact grassland: *Agropyron–Poa*, Garfield Co., Wash.	0.779	17.7
3	Prairie rich in species: *Sporobolus-Andropogon*, N.D.	14.3	89.3
4	Heath with few species: *Calluna* at Ø sterhede, Jutland	22.0	3.66
5	Relatively rich heath: *Dryas* on Mt. Njulja, Lapland	21.3	16.9
6	Herb ground-cover under forest, Antrim Co., Mich.	65.8	34.4
7	Chamise–sage chaparral, base of Mt. Lowe, Calif.	274	14.6
8	Old-growth white pine, Vilas Co., Wis.	860	8.4
9	Old-growth mixed forest: Brownfield Woods, Ill.	4 015	18.3
10	Primary rain-forest, Kamerun: Johann-Albrechts Höhe	6 065	132.6
11	Mora forest of stream-borders, British Guiana	21 650	100.7

THE GEOMETRY OF S-CURVES

Imagine a "standard S-curve," with reference points R, M, and F at smallest representative area Ar, minimum area Am (= 5 Ar), and area of "fair-sized stand" Af (= 50 Ar). The species numbers at these areas are Sr, Sm (which for present purposes can be put at 1.48 Sr), and Sf (= 2 Sr). The coordinates of the three reference points can be shown in positions which suggest those on the curve, thus:

Af, Sf
Am, Sm
Ar, Sr

We can readily perceive the differences between two curves, or the effects of changing a standard curve, if simple numerical values are assigned:

5000, 20
500, 14.8
100, 10

1. If species-numbers at the stated areas are increased in the same ratio (say 3/2), the curve is made steeper, and reference areas are not changed:

5000, 30
500, 22.2
100, 15

Reducing species-numbers by a constant ratio makes the curve less steep, and similarly does not change reference areas.—Changing species-numbers by a constant increment, as by raising the curve 2 species at all areas as large as 100, makes it necessary to compute new reference points. The new reference areas will in this case be smaller.

2. A shift of the whole curve to right or left increases or decreases all three reference areas in the same ratio, and does not change species-numbers. A shift to right through a distance representing the logarithm of 1.5 gives these coordinates:

7500, 20
750, 14.8
150, 10

3. If it is assumed that the flex point is at R in the "standard curve," consider the effect of changing the curve so that flex point is now above R. On a "standard" graph, the flex point was moved up on the curve from (100, 10) to (160, 11.5). On the readjusted curve (lower part moved upward and leftward), the

changed reference points were found by trial and error, with Sm read from the new Am (= 5 Ar). They are:

4480, 19.78
448, 14.48
89.6, 9.89

Reference areas and species-numbers are reduced, the degree of convexity between R and F is less, and the ratio of Sm to Sr is correspondingly reduced from 1.48 to 1.469.

4. If a curve is made steeper or less steep (as by rotating it on one of the reference points) what are the effects? In a trial operation, a standard curve was pivoted on F and rotated clockwise, raising its lower part until the point that had been R was at 92, 11; and what had been M was at 476, 15.47. To readjust the lower section, the convex part was extended downward to a new flex point at 50, 9.08; and a new concave section was fitted to the curve. New reference points were found, as follows:

3000, 19.28
300, 14.3
60, 9.64

The operation made the curve less steep, and the effect is, as in the preceding case, to make reference areas smaller. The new R is in this instance above the flex point, and convexity between R and F is more pronounced, as shown by the ratio of Sm to Sr, which is now 1.484.

If rotation on R or on M had similarly made the curve less steep, reference areas would likewise have been reduced from original values. If rotation on any point between R and F makes the curve steeper, the reference areas become larger. If the upper part of the curve is raised or shifted to the left, reference areas likewise become larger.

5. Reducing the convexity of the upper section of the curve (with no change in the lower section) makes the upper part steeper, and has the effect of moving the reference points upward on the curve. Conversely, greater convexity moves the reference points downward, giving smaller reference areas with fewer species.

One can usually judge by casual inspection of two curves, considering position to right or left, steepness, and degree of convexity, which of the two is likely to have the larger reference areas. We may now consider some characteristics of communities which affect the position and form of curves and thus the size of reference areas. Thus larger plants yield a curve that is farther to the right; floristic richness makes higher and steeper curves; persistence of rate of species-increment into large areas makes a smaller degree of convexity, steeper upper section, and larger reference areas.

FACTORS INFLUENCING THE SIZE OF REFERENCE AREAS

1. Size of plant individuals or clumps. This is the leading influence in determining extent of reference areas. We should expect lichens or mosses to form the smallest self-contained units of land vegetation; old-growth forests with giant trees, the largest. The community with the smallest lichens does in fact have a smaller minimum area than any formed of larger lichens, and there is a gap between lichen communities and the finest grassland. (The smallest minimum area found for any grassland is 0.48 mlc. for Gilomen's alpine Caricetum mucronatae. This value is not used in Table 26 because of its uncertainty, but the possibility of its being even smaller than 0.48 is not questioned.) As seen with results from the Danish Maglemose, moss-clumps in bogs may be so large that reference-areas have little relation to the small size of individual moss-plants.

Importance of some of the other factors may be gauged from these facts: Although Am for a mixed deciduous forest with giant trees (some reaching 50 inches d.b.h. or larger) may be only 2.5 acres (2761 mlc. in Cox Woods), and possibly as small as 1.5 acres in old-growth mixed conifers, yet the largest Am-value found in tropical forest with perhaps smaller tree-sizes, is over 21.5 acres. This spread, probably more than ten-fold, is due to factors other than size of plants. It is likely that some of these factors work in the direction of reducing rather than increasing minimum area.

2. Marked domination by one or a few species. It is apparent that if the dominants occupy 95% of the space in one stand and 80% in a nearby similar stand, it should take about 4 times as large an area in the first stand as in the second to give equal representation of additional species. Concrete illustrations were encountered in this study. Thus, in Burchardt's tropical forest on Fernando Po, 2 top-story and 2 understory species have 197 trees of the given count of 237. Its Am is slightly larger than the mean for 7 richer West African forests having on the average over 4 times as many species (Am 5690, 5628; Sm 29.6, 127.7).—In the bush near Mt. Lowe, *Artemisia californica* and *Eriogonum fasciculatum* strongly dominate. In an Am of 134 mlc., only 6.9 spp. occur. The larger but more equably mixed shrubs of oak chaparral have an Am of 79 to 262 mlc., with 19.7 to 22.6 spp.—Of the herb covers under shady forest, that dominated by *Anemone nemorosa* under beech at Jonstrup Vang has an Am so much larger than the usual range for the group (116 mlc. as compared with 81.7, next highest) that it was omitted from Table 26.—The *Carex lasiocarpa* bog in northern lower Michigan has an Am of 100 mlc., many times as great as any of the other 3 sedge bogs studied.

3. Low density. Scatteredness or wide spacing of individual plants has the same effect as actual size, increasing the area required for sufficient representation of a community. Examples described earlier include the culled mixed deciduous forest at Robinson, Illinois, the grassy parang of Mindoro, the blowsand and some other sand-prairie examples, and the desert shrub of *Larrea*.—High density

works in the other direction. Conditions which tend toward greater numbers of small individuals will be mentioned with other factors.

4. Quality of site. Degree of productiveness of a habitat works in several different ways to influence size of reference areas. The very poorest or most highly specialized sites may permit occupation by only one or a few species, with usual requirement of large area for adequate representation of less abundant species. Some of the poorer heaths and bogs, rocky areas, sterile sandy lands, tropical heath forests or wallaba forests, and salt flats with *Sarcobatus*, etc., may be recalled.

The least favorable climates may give the same result, with relatively large reference areas considering the sizes of plants and the numbers of species capable of growing in the area. Here may be mentioned semi-arid bush communities, again the desert shrub of *Larrea*, the mountain forests of low latitudes. But poor climate may not prevent the development of quite rich communities, as the *Vaccinium–Dryas* heath with herbs on Mt. Njulja, above the Arctic circle.

In general the best sites (soil and topography) are more likely to be rich in species and to have relatively small reference areas, although the somewhat below-optimum sites may surpass them through such a set of circumstances as the following: Among Jentsch's primary Kamerun forests, the stand at Ngongnkeng (Plot VIII) is richest in species (see Table 6). It has 162.2 spp. on 5592 milacres. Of five other primary stands, two (at Mujuka and Bekili) have smaller reference areas, but have many fewer species on these areas. If we use density of tree individuals as a criterion of site quality (it is well known that on better sites competition results in bigger and thus fewer trees per acre), we find highest density in the Ngongnkeng stand, 251 per acre (3″ diam. limit). Density for the five other stands is 136.5 to 242.9 per acre, with the mean at 187.3. The mean Am for the five stands is 6556 mlc., larger than for No. VIII. The 6556 milacres may represent a usual minimum area for good quality West-African forest. The probably inferior stand at Ngongnkeng has richer mixture of species and smaller minimum area partly because its site is less favorable and its trees smaller and more numerous.

5. Extent and form of site. A small or narrow area of a particular habitat surrounded by site conditions favoring other kinds of vegetation may have fewer species of its own community and a larger infiltration of species from its neighbors than would the same-sized area within a large expanse of its own kind. Several examples in this study may be cited: the narrow alluvial flat in the Verdugo hills, covered with bush but with strong infusion from neighboring chaparral hills; Potzger and Friesner's ridge-top forests, with rather rich complement of tree species from neighboring slopes of different exposures; Jaccard's Pierrier de Sandalp, a narrow pebbly bench; river-edge forests, such as the mora type as described by Davis and Richards; narrow bluffs or ridge-slopes, as the greenheart type of the same authors. The effects on reference areas are not usually simple, but to the extent that exposure to infiltration from other types

favors continued rate of species-increment at large areas, the reference areas are larger than they would be otherwise. This is obviously the case in the Verdugo Hills flat and the Pierrier de Sandalp.

6. Environmental diversities. Jaccard was probably the first to explain that strong differences of substratum and of topography, notable in certain mountainous districts, are accompanied by similar diversities of floras and of vegetation-units. The total flora of a district, as well as the strictly local flora of any moderately homogeneous area which is not too unfavorable to a majority of the species within range, should be richer because of this environmental diversity. The usual effect upon species-area characteristics of a stand in such a district is probably to increase somewhat the reference areas, but to increase the numbers of species at those areas in a higher ratio.

Diversities within a site, caused by microrelief, rocky ground, and the strong contrasts incidental to much-dissected surfaces (most strikingly described by Skottsberg in one of his accounts of Juan Fernandez), cause the development of complexes rather than uniform associations. Although more species are present on an acre or hectare, the effects on reference areas are not easy to comprehend. It is usually expedient to study separately each of the more important synusiae or phases or layers. Comparison of each of these with its closest equivalent in a nearby homogeneous setting has not thus far been attempted, but should help toward the understanding of a complex.

7. Degree of complexity of a community. It is necessary only to mention that a community regularly possessing two or more layers or phases will have more species, and perhaps on that account requires greater area for their adequate representation than a simpler one-layer community. Reference areas for a particular phase or layer may be larger because of discontinuity of that phase or layer, due to the occupation of space by other parts of the community.

8. Floristic richness. In itself, the presence of large numbers of species on one homogeneous area has a limited effect in increasing minimum area. In several groups of related communities, curves drawn on the same sheet show great differences in steepness, some with 5 or 6 times as many species as others, but with small differences in size of reference areas. It is true that the physical space-requirements of the greater number of individuals to give a greater number of species, in accordance with the hollow-curve principle, make the minimum area of a highly-mixed forest or prairie larger than that of a simple mixture; but as intimated, this effect is limited. It is greatly exceeded by the effect of floristic richness, not so much of a particular stand or sample area, as of the district and region. It is this richness, of what statisticians would call *the supply* (of additional species), which is chiefly responsible for the often mentioned persistence into large areas of the rate of species-increment. Its effect on the curve is to reduce convexity between R and F (as well as above F), and so to shift reference points to high positions. Grassland and tropical-forest floras of certain regions may thus each constitute a rich supply of species for many of their communities.

9. Proportions among species. This may seem to be the same topic as degree of domination, but among dominants as well as among other species there are great differences in proportions. These are most readily seen in the hollow-curve type of graph, in which the species are shown in successive positions, each species represented by an ordinate showing its numbers in a specified area, its frequency of occurrence in plots, or some other quantity. Some J-shaped curves of this kind are deeply hollowed. In a more nearly equable distribution, the leading few species are not so greatly more numerous than the next ones; the curve is not deeply hollowed; many species occur in a small total of individuals (the α-value, or index of variability, is high at the area to which the curve applies); reference areas for the community are small and species-numbers at those areas are high. Some heath, bush, and chaparral communities may show a hollow curve in which the 2 or 3 leading species occur with smaller than usual disparity of numbers, but in which a considerable gap exists between these and the other species, and possibly also there is much disparity of numbers among the others. Such a community will have a large minimum area. The characteristics of communities and their stands which the hollow-curve type of graph may reveal are often explainable, and deserve attention in future studies of vegetation.

10. Stage of development of community. A young even-aged forest stand may have one, a few, or many tree species, depending on opportunities for invasion from surrounding areas, as well as on development from sprouts or from seeds in the ground before destruction of the earlier stand. Competition may eliminate species present at first, or new species may enter as time goes on, or both of these may happen. Changes in richness therefore must be studied separately in each stand as it develops. However, without any actual change in the composition of a stand, it is likely to have smaller reference areas if its trees are young and closely spaced.

Similar considerations will usually apply to other types of communities. If the three grasslands at Maalov Krat could be interpreted as three stages of a uniform development (not a safe procedure), reference areas become smaller between one and eight years after the fields are permitted to revert to weeds and to the herbs and grasses from nearby meadows and from the Markskellene (the unplowed border strip, relatively undisturbed and stable). If after some further years of development, the grassy fields become quite like the Markskellene in composition and in texture, they should similarly have reference areas much larger than in the one-year field. One can imagine the vegetative spread of grass-mats and of certain dicot herbs, which increases the average ground-space per plant and so tends to enlarge the reference areas. During these same years numerous additional species enter, giving, as in the Markskellene, a large Sm-value. (Details are seen in Table 17 and the description just following it.)

11. Condition of stand. Areas showing differing degrees of interference by man or by grazing animals, or different conditions in the same stand at various times, require evaluation in their effects on size of reference areas and

in richness of composition. Usually the effects are cumulative, in the direction of deterioration, and of reducing the number of species, perhaps until only a very few opportunist species remain. Natural causes, as fluctuations within the rainfall cycle, or prolonged immunity in certain places from over-grazing or from fire, may also affect condition of stand. Changes in density may often be easiest to evaluate.

IMPLICATIONS OF CERTAIN RESULTS

The most useful application of findings as to size of reference areas will probably be in selection of sample-plot sizes, in many types of applied ecology; forestry, range ecology, soil conservation, etc. Comparisons of the numerous types of communities studied and of the different examples in any one group may suggest trial plot-sizes which further experience will later modify. While economy of sampling will continue to require the use of many small separated plots, it is recommended that at least one sizable one-piece area be investigated also, to the extent of obtaining a reasonably complete census of species present. This should be as large as minimum area, or if practicable, ten times minimum area (the size of Af). In this way, materials will accumulate for an understanding of the still too little known differences between composition as shown by an aggregate of small plots or by line or strip survey, and that of a sizable one-piece area.

The writer has been repeatedly impressed by the value of definite and comprehensive sets of plot data, especially when essentials for individual plots are included, as can often be done in relatively small space. Maps of quadrats and larger plots are particularly useful. These source materials can be of great value in many ways that are quite unpredictable. Definiteness of statement as to size-limit of trees or plants included, and as to size of area surveyed in an Aufnahme or in a listing of species present, is especially recommended.

There is a growing list of useful botanical descriptions of little-known vegetation-types in many parts of the world by observant collectors and by experienced systematic botanists, foresters, geographers, and other travelers. If, in as many such descriptions as practicable (as well as in articles by ecologists and geobotanists), a definite account can be given of the content of a stated homogeneous area representative of its type, their value will be greatly increased. It may be possible to give a supplementary list of additional species seen in a larger specified area of the same type. Precise identification is not required for all species.

On the whole, the reference areas tentatively determined in this study have proved to be smaller than was expected. As several times mentioned, the Am-value or minimum area seems to be rather conservative, in that it includes more than is usually required for minimal area or Minimiareal by different investigators. If this is so, Ar or one-fifth the Am size may prove to be sufficient for many purposes. But as suggested in an article by Richards on tropical forests

(1945), it is not to be expected that in highly-mixed types, different sizable areas will be closely alike in composition, particularly if they are well separated. This is true even if the areas are several times as large as Af, the "fair-sized stand," equal to 10 Am.

One implication of this small size of reference areas may be of use in efforts by biologists and conservationists to preserve areas of natural conditions and remnants of vanishing types of plant cover with their animal inhabitants as well. So far as plants and smaller animals are concerned, a preserved area as large as 1 to 10 Am is truly representative of its type. Even in old-growth forest with Am values up to 4 acres in deciduous mixed types and up to 10 or 20 acres in tropical mixed types, an area of Am size is worth preserving. It is true that the smaller the area, the greater are the hazards to which even its further study by investigators may subject it. The preservation of several small areas instead of only one may reduce the hazards. It is easier to see that a surviving prairie remnant no larger than 5 to 15 milacres is worth preserving, if we know that this size may exceed the minimum area. Again, as with tropical forests, the more numerous such remnants can be, the better, since no two need be expected to be closely alike. A 10-milacre prairie might have such dimensions as 5×8.1 meters, or 17.4×25 feet, or 20×21.8 feet. It is even possible to reconstruct a sample of a desired type of grassland. A "synthetic" prairie (or other vegetation) could be established where it might be desired, in park, museum ground, botanical garden, or university study-plot, by transplanting, seeding, and for a considerable period, weeding by hand. A small, carefully-tended sample of natural or synthetic vegetation is better than a large one which cannot be maintained.

Another implication of the usually small size of reference areas may bear on problems of classification of natural units of vegetation. Various students of vegetation have quite different opinions as to the extent and degree of unity of plant associations, and as to the number of kinds of natural units that should be recognized and named. The smaller the areas required to exhibit the characteristics of types, and the greater the variations shown in these small areas, the more likely it is that there are very large numbers of types, readily distinguishable and in many cases worthy of recognition. The minimum extent of a stand is suggested by the size of reference areas for a type. The minimum extent of the aggregate of all stands referable to one type is similarly pertinent to this problem of the extent and number of associations or other vegetation units. The writer has collected much information bearing on the problem. An abstract of a preliminary presentation (at St. Louis, March, 1946) may be found in *Bull. Ecol. Soc. Am.* 27 (1) : 15.

The close relations between species-area studies and the problems of floristic richness are ably treated in Richards' article on tropical rain forest (1945). The present study has brought to light some complications in the definition and expression of such indices of floristic richness as the Mischungsquotient (mean number of tree individuals per species). This index is not wholly adequate; of

several tropical forests, No. 1 may be richest by one standard, No. 2 by a second, and No. 3 by a third. Materials toward clarification of such standards were accumulated in this study, but do not belong in the present report.

HYPOTHESES TO EXPLAIN SPECIES-AREA CURVES

This subject is closely connected to the next one, the need for additional studies. As the reader will have concluded, the principal need in further elucidation of species-area relations, whatever system of coordinates is used in showing them graphically, is rational explanation, with incorporation of important factors into an equation for a species-area curve. There is no reason to doubt that considerable progress in mathematical parts of the problem will be made before long. Those interested will find much of value in the articles by Romell (1920, 1923, 1925, 1926, 1930), Brenner (1921), Svedberg (1922 *a* and *b*), Nordhagen (1923), Kylin (1923 *a* and *b*, 1926), Wicksell (1924), and Teräsvuori (1927). (The last includes valuable materials which should be further analyzed.) Three assumptions of Romell (1930: 591) are considered to be especially likely to lead to further mathematical insight. Romell states: "The only theoretical curves which . . . check satisfactorily with empirical findings . . . seem still to be those deduced from a *normal curve of variation* (or rather a set of such curves), making three simple and clear assumptions. . . . Every one of the species is adapted to a definite site; . . . the site factors in the area or district analyzed vary from point to point according to pure chance around a mean value; . . . on the average it is just as probable to have species adapted to the rarer combinations of site factors as to those commoner in the particular area." The third assumption is amplified in a footnote. It may not be superfluous to recall a fourth (which may be implicit in Romell's first): each species is more or less plastic: it has an amplitude of toleration above and below a mean value representing the "optimum" of each factor affecting it. Whether these assumptions are sufficient for communities exhibiting strong competition is another question to be considered.

Two other mathematical approaches may be suggested. Both are based on the hollow-curve principle. One is the investigation, already well advanced, of Fisher's series dealing with numbers of species in relation to numbers of individuals. (See Fisher, Corbet, and Williams, 1943; and Williams 1944). This series makes use of the number of what may be called the "tail-end" species: those which in a given collection (of insects, in most of the materials reported) are represented by a single individual. Empirical hollow-curve findings from plot data for vegetation (encountered in the present study) suggest that fewer plant species are represented each by one individual than one would expect from Fisher's series. As earlier intimated, established populations of rooted plants appear to be influenced by factors additional to those affecting the insect materials studied by Corbet and Williams.

An empirical approach to the understanding of the properties of hollow curves

might consist in the construction of a graduated series of such curves from new field data for each of several different kinds of vegetation. Each plot will yield its own hollow curve for numbers of individuals of the different species present. The normal character of a curve for a given plot-size can be determined from study of many curves for individual plots of that size. If the normal curve for each plot-size of a graduated series is thus found for a particular vegetation, and if the study is repeated for different vegetations, materials for other types of mathematical analysis of hollow curves will be available. The form of empirical hollow curves for plant communities will probably depend more upon leading species than upon tail-end species. "Degree of hollowness" will be slight in equable mixtures, pronounced in communities showing strong domination by one or a few species. Further information on hollow curves will be found in the article by Fisher et al. (1943) and in works there cited. Earlier emphasis on hollow curves is well known through the writings of J. C. Willis. See Willis and Yule (1922); Willis (1940). A paper by J. C. Chamberlin (1924) is notable.

A mathematician may perceive further points of attack upon species-area problems from the writer's hypotheses to account for the nearly straight and the obviously convex sections of S-curves. Consider first the small-area end of a curve for forest. It was expected that at a plot-size equal to average ground-space per tree (N or mean number of trees per plot $= 1$), the mean species-number, S, would also be 1. But some plots of this size have 2 trees; in half or more of these plots both trees belong to the most abundant species; and other plots have no trees. On the average, S is slightly less than 1 when $N = 1$, so far as present experience indicates. Similar considerations apply to types other than forest.

The tail of the curve, if much prolonged into smaller areas than that at which $N = 1$, approaches zero. In the other direction the concave section of the curve becomes steeper as far as the flex point. The concavity is a consequence of plotting area on a logarithmic scale, since the S/N ratio decreases progressively from the smallest areas onward. Curvature is slight in the vicinity of the flex point, which means that species-increment continues at nearly the logarithmic rate expressed by the slope at the flex point, up to a plot-size at which convexity of the curve becomes apparent.

Persistence of fairly rapid rates of species-increment from small areas to beyond the flex point may be explainable from the following considerations: (1) Even in fairly homogeneous sites there is perceptible variability of site conditions from spot to spot, as stated by Romell. Some of this is due to basic physical diversities of soil or of surface; some is due to plant or animal reactions, as in shading by bushes or in spotty occurrence of decaying stumps or of animal burrows. (2) There is also a partially independent variability of plant cover due to vagaries of plant distribution. It results partly from chance location of the spots which individuals of any species were able to reach and to colonize, partly from aggregation by local seeding and vegetative spread. (3) The space-scales

of these environmental and plant-location diversities vary, partly with sizes of plants, partly otherwise. In some communities the mosaic of variabilities is predominatingly fine-textured, in others coarse-textured but in any community there are both large-scale and small-scale inequalities of environment and of plant cover. Romell's 1930 paper shows clear recognition of the existence of a prevailing texture of variability. A sufficiently coarse texture makes the vegetation a complex rather than an association. Romell states (p. 593): "At least very often, the 'homogeneity' . . . consists of a sufficient 'regularity' and a sufficiently short 'wavelength' of the recurring variations in the composition of the plant cover, rather then in a thorough mixing of the elements of the vegetation so as to form a uniform carpet. . . ."

The rapid increase in species-numbers at very small areas is due to addition of space for enough individuals to represent more than the one or two species first included. After the two or three commonest species are present, the next increments are due to variabilities of plant cover. As more and more kinds of the smaller pieces of the mosaic, and later as larger pieces are included, more and more species are represented in the area attained. Variations of the general pattern are still being added at areas some distance beyond the flex point. At an area at which convexity of the curve has for some distance been apparent (about at Am or minimum area), the common variations have already been included; beyond Af further additions are chiefly of rare species. Only a rich supply of additional species from surrounding territory, or the encountering of new and different variations of site and of plant cover, will determine a curve which ascends with little convexity into strikingly large species-numbers. Although the different sections of a species-area curve are more readily visualized if the area scale is logarithmic, the above considerations apply also to curves plotted to two linear scales. On these curves also, reference points can be found by trial and error.

ADDITIONAL STUDIES NEEDED

Of particular species-area problems in need of further study, new field data for communities of few species should settle the already-mentioned questions whether some curves fail to yield twice as many species at fifty times the area, and whether some heaths and bogs may have "double curves." These, if found, may show initial ascent of the curve through areas smaller than one square meter, to a nearly level section with very small increment of species, succeeded by a second steeper section of the curve as less common species are included. (See the account of Russian bogs). Study of impoverished communities in which an absolute limit in species-number may be reached (at least for certain stands) should also be made. These show a "curve of saturation," in which, as in one curve for saline flats with *Sarcobatus,* the upper section is a horizontal line. Some of these, if large-enough areas are available, may be found to have "double curves."

Certain kinds of vegetation whose species-area relations are practically unknown include two-phase grass-and-tree combinations, open forests, tropical grasslands, Mediterranean and Californian grasslands, South African grasslands and those of temperate South America; most types of vegetation in Australia and New Zealand; Amazonian forests, mountain forests in South America; moss communities in bogs, on cliffs and other rock surfaces and on tree bark; desert communities. Many types of temperate forests, especially of conifers, have received little attention. Direct comparisons of shrub or of ground layers in different forests will be improved if field data for species-area purposes are obtained in the same manner.

As to improvement of field methods in species-area studies, one can recommend: determination of species-numbers in larger and more numerous one-piece areas of graduated sizes; if practicable, determination or estimation of density as well as of species-numbers; in forests, use of 7-cm., 3-inch, 10-cm., or 4-inch diameter-limits, with provision of data for dependable conversion from the limit used to any of the others; more general construction of plot-maps; and study of at least 50 plots of the smallest size chosen (these have greatest variability in species-number and in other characteristics). More general publication of plot-maps and of data for individual plots is also highly desirable.

BIBLIOGRAPHY

ARRHENIUS, O.

1923. Statistical investigations in the constitution of plant associations. Ecology 4: 68–73. [BEUMEE'S ground-vegetation in teak forests, Java; p. 69, Table 3.]

BAKER, J. R.

1938. Rain forest in Ceylon. Kew Bull. 1938: 9–16.

BENEDICT, AUDREY HOPE

1945. Normal diameter-distribution and mortality in all-aged mixed forest. 39 pp. Thesis, Univ. Ill.

BERGEN, J. Y.

1903. The macchie of the Neapolitan coast region. Bot. Gaz. 35: 350–362, 416–426.

BERTIN, A., avec la collaboration de M. BETTENFELD et R. BENOIST

1920. Les bois de la Guyane française et du Brésil. (Mission Forestière Coloniale, Tome Cinquième.) 318 + 3 pp. Paris, E. Larose. [The tables of prospections occupy pp. 7 to 32.]

BEUMÉE, J. G. B.

1922. Floristisch-analytische onderzoekingen van de korte flora in kunstmatig aangelegde djatiplantsoenen op Java, in verband mit de ontwikkeling van den djati-opstand. 166 pp. Dissertation Wageningen. [Original not seen. Data from ARRHENIUS, 1923.—Abstract by MARKGRAF in Bot. Jahrb. 58 (H. 2): Litb. pp. 45–46. 1923.]

BRADLEY, S. RAY

1932. Forest distribution in Crawford County, Illinois. 29 pp., 4 maps. Thesis, Univ. Ill.

BRAUN, J.

1913. Die Vegetationsverhältnisse der Schneestufe in den Rätisch-Lepontischen Alpen. Neue Denkschr. Schweiz. Naturf. Ges., vol. 48. 7 + 347 pp., 4 pls., map. Zürich.

BRAUN-BLANQUET, J.

1932. Plant sociology. The study of plant communities. Translated, revised and edited by GEORGE D. FULLER and HENRY S. CONARD. 439 pp. New York, McGraw-Hill.

BRENNER, WIDAR

1921. Växtgeografiska studier i Barösunds skärgard. I. Allman del och floran. Acta Soc. Fauna Flora Fenn. 49 (5): 1–151, fold. map, 1: 100,000.

BROWN, WILLIAM H.

1919. Vegetation of Philippine mountains. The relation between the environment and physical types at different altitudes. Dept. Agr. & Nat. Resources, Bur. Sci., Manila, Publ. 13. 434 pp., 41 pls., incl. map of Mt. Maquiling.

BROWN, WILLIAM H., and MATHEWS, DONALD M.

1914. Philippine dipterocarp forests. Phil. Jour. Sci. 9 (A): 413–561, pls. 1–13, map.

BURCHARDT, H. *See* MILDBRAED, 1933.

BURKILL, I. H.
1919. The composition of a piece of well-drained Singapore secondary jungle 30 years old. Gardens Bull., Straits Sett. 2: 145–157.

CAIN, STANLEY A.
1934. Studies on virgin hardwood forest: II. A comparison of quadrat sizes in a quantitative phytosociological study of Nash's Woods, Posey County, Indiana. Am. Midl. Nat. 15: 529–566.

CHAMBERLIN, J. C.
1924. Concerning the hollow curve of distribution. Am. Nat. 58: 350–374.

COOPER, G. PROCTOR, 3d, and RECORD, SAMUEL J.
1931. The evergreen forests of Liberia. . . . Yale Forestry Bull. 31. 11 + 153 pp., 8 pls., map.

DAHLGREN, B. E.
1937. [Abstract of SOBRINHO, 1937.] Trop. Woods No. 52: 37–38.

DAUBENMIRE, REXFORD F.
1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecol. Monogr. 12: 53–79.

DAVIS, T. A. W., and RICHARDS, P. W.
1934. 1933. As for Richards, P.W. The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest. Jour. Ecol. 21: 350–384; 22: 106–155.

DE CANDOLLE, ALPHONSE
1855. Géographie botanique raisonée . . . 2 vols., 1–606, 607–1366 pp. Paris, Victor Masson; and Genève, J. Kessmann. (Chapitre VII. De l'aire des espèces, pp. 474–606. Significant statements as to floristic richness and extent on p. 1275, following the table "Exposé des faits.")

DU RIETZ, G. EINAR
1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. 272 pp. Akad. Abhandl., Upsala (Wien, A. Holzhausen).
1924. Zur Klarung einiger historisch-pflanzensoziologischen Streitfragen. Bot. Notiser 1924: 425–439.

DU RIETZ, G. E., FRIES, TH. C. E., OSVALD, H., und TENGWALL, T. A.
1920. Gesetze der Konstitution natürlicher Pflanzengesellschaften. Flora och Fauna 7. 47 pp., 5 fold. pls. Uppsala und Stockholm, Almqvist & Wiksells.

FERDINANDSEN, C.
1916. Ekskursionen til Hammer Bakker, Store Vildmose og Øland den 25.–27. Juli 1915. Bot. Tidsskr. 34: 191–202. [Alvar vegetation.]

FINK, BRUCE
1903. Some talus Cladonia formations. Bot. Gaz. 35: 195–208.

FISHER, R. A., CORBET, A. S., and WILLIAMS, C. B.
1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Jour. An. Ecol. 12: 42–58. (Part 1, CORBET. Results obtained with Malayan butterflies, pp. 42–44.—2, WILLIAMS. Results obtained by means of a light-trap at Rothamsted, pp. 44–53.—3, FISHER. A theoretical distribution for the apparent abundance of different species, pp. 54–57.—Summary, p. 58.)

GILOMEN, HANS
1926. Neuere Methoden zur Untersuchung der Pflanzengesellschaften. Mitteil. Naturforsch. Ges. Bern 1925: xix–xxi.

GISIN, HERMANN
1945. Minimalraum und Homogeneität edaphischer Lebensgemeinschaften von Apterygoten. Verhandl. Schweiz. Naturforsch. Ges. 1944: 140–141.

GLEASON, HENRY ALLAN
1907. (See HART and GLEASON)
1910. The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. Nat. Hist. 9 (3): 19–174, pls. 1–20.
1920. Some applications of the quadrat method. Bull. Torr. Bot. Club 47: 21–33.
1922. On the relation between species and area. Ecology 3: 158–162.
1925. Species and area. Ecology 6: 66–74.

GRIFFITHS, DAVID
1904. Range investigations in Arizona. U. S. Dept. Agr., Bull. 67, 62 pp., 10 pls.

HANSON, H. C., and WHITMAN, W.
1938. Characteristics of major grassland types in western North Dakota. Ecol. Monogr. 8: 57–114.

HART, CHARLES A., and GLEASON, HENRY ALLAN
1907. On the biology of the sand areas of Illinois. Bull. Ill. State Lab. Nat. Hist. 7 (7): 133–273, pls. 8–22, map. (Part II, pp. 149–194, is Gleason's botanical survey.)

HOLTTUM, R. E.
1924. The vegetation of Gunong Belumut in Johore. Gardens Bull., Straits Sett. 3: 245–257.

HORTON, JEROME S.
1941. The sample plot as a method of quantitative analysis of chaparral vegetation in southern California. Ecology 22: 457–468.

HUECK, K.
[MISCHUNGSQUOTIENT.] Hueck is mentioned by MILDBRAED, 1930, Ber. d. bot. Ges. 48: Beih. pp. (55)–(56), as having suggested the term (in conversation). It is the ratio of number of species to number of trees (with specified diameter limit) on a stated area.

JACCARD, PAUL
1902. Lois de distribution florale dans le zone alpine. Bull. Soc. Vaud. Sci. Nat. 38: 69–130.—(P. 89: "8. La richesse florale fonction de l'étendue.")
1908. Nouvelles recherches sur la distribution florale. Bull. Soc. Vaud. Sci. Nat. 44: 223–270, pls. 10–20.
1914. Etude comparative de la distribution florale dans quelques formations terrestres et aquatiques. Rév. Gen. Bot. 26: 5–21, 49–78.

JÄGGLI, MARIO
1928. La vegetazione del Monte di Caslano. Viertelj. Naturf. Ges. Zürich 73, Beibl. (Festschrift Hans Schinz): 252–285.

JENNY-LIPS, H.
1930. Vegetationsbedingungen und Pflanzengesellschaften auf Felsschutt. Phytosoziologische Untersuchungen in den Glarner Alpen. Beih. Bot. Centralbl. 46 (Abt. 2): 119–296.

JENTSCH, DR.
1911. Der Urwald Kameruns, Folgerungen aus den auf der Expedition 1908–09 gewonnenen Erfahrungen in Bezug auf den Zustand und die Nutzbarmachung des Waldes. Beih. Tropenpflanzer 12: 1–199.

KATZ, N., und KATZ, S.
1926. Zur Prüfung und Kritik einiger Konstanzgesetze der Upsalaer soziologischen Schule. Bot. Notiser 1926: 189–200.

KELLER, BORIS A.
1927. Distribution of vegetation on the plains of European Russia. Jour. Ecol. 15: 189–233.

KENOYER, LESLIE A.
1927. A study of Raunkiaer's law of frequence. Ecology 8: 341–349.

KYLIN, HARALD
1923a. Växtsociologiska randanmärkningar. Bot. Notiser 1923: 161–264.
1923b. Växtsociologiska betraktelser. Bot. Notiser 1923: 451–456.
1926. Über Begriffsbildung und Statistik in der Pflanzensoziologie. Bot. Notiser 1926: 81–180.

LINKOLA, K.
1922. Zur Kenntnis der Verteilung der Landwirtschaftlichen Siedlungen auf die Böden verschiedener Waldtypen in Finnland. Acta For. Fenn. 22 (3): 1–64.

MALINOWSKI, EDMUND
1911. "Krzywa" Jaccard'a a łąki podkrakowskie. [La "courbe" de Jaccard et les prairies des environs de Cracovie.] (z 2 rycinami w tekście). Kosmos 36: 330–336.

MARBERRY, W. M., MEES, J. D., and VESTAL, A. G.
1936. Sample-plot statistics in University [Trelease] Woods. Trans. Ill. Acad. Sci. 29: 69–71.

MARKGRAF, FR.
1923. [Abstract of dissertation by BEUMÉE, 1922.] Bot. Jahrb. 58 (H. 2): Litb. pp. 45–46.

MCCOY, SCOTT
1939. A phytosociological study of the woody plants constituting 25 type forests of the Illinoian till plain in Indiana. Proc. Ind. Acad. Sci. 48: 50–66.

MERRITT, MELVIN L.
1908. The forests of Mindoro. Philippine Bur. Forestry, Bull. 8. 51 pp., map.

MILDBRAED, J.
1930a. Zusammensetzung der Bestände und Verjüngung im tropischen Regenwald. Ber. Deutsch Bot. Ges. 48: Beih. (50)–(57).
1930b. Probeflächen-Aufnahmen aus den Kameruner Regenwald. Notizbl. Bot. Gart. Berlin-Dahlem 10: 951–976.
1933. Ein Hektar Regenwald auf Fernando Poo, aufgenommen von H. Burchardt. Notizbl. Bot. Gart. Berlin-Dahlem 11: 946–950.

MUNNS, E. N., and OTHERS
1935. Sample plots in silvicultural research. U. S. Dept. Agr., Circ. No. 333. 91 pp. (By the Division of Silvics, Branch of Research, Forest Service, with cooperation by committee of Soc. Am. Foresters.)

NETTO, F. F.
1945. The problem of the Amazon—I. Sci. Mo. 61: 33–44.

NORDHAGEN, ROLF
1923. Om homogenitet, konstans og minimiareal. Nyt. Mag. f. Naturvid. 61: 1–51.

NOSKOVA, T. A.
1923. Om homogenitet, konstans og minimiareal. Nyt. Mag. f. Naturvid. nogo Siezda Botanikov 1928: 253–254.—Biol. Abstr. 6: Entry 21350. 1932. Abstract by G. A. LEBEDEFF.

OLSEN, CARSTEN
1920. Maglemose i Grib Skov. Undersøgelser over Vegetationen paa en nordsjællandsk Mose. Ved Henning E. Petersen. V. Mosvegetationen. Bot. Tidsskr. 37: 23–47. [Parts I to IV are in vol. 36, pp. 57–154, with maps, photographs, and tables of occurrences in plots of higher plants. 1919.]

OOSTING, HENRY J., and REED, JOHN F.
1944. Ecological composition of pulpwood forests in northwestern Maine. Am. Midl. Nat. 31: 182–210.

PALMGREN, ALVAR
1917. Studier öfver löfängsområdena på Åland. Ett bidrag till kännedomen om vegetationen och floran på torr och på frisk kalkhaltig grund. III. Statistisk undersökning af floran. Acta Soc. Faun. Flor. Fenn. 42 (1): 475–634, 2 diagrams, 8 fold. tables, 2 maps.
1922. Über Artenzahl und Areal sowie über die Konstitution der Vegetation. Eine vegetationsstatistische Untersuchung. Acta For. Fenn. 22 (1): 1–136, 2 diagrams, 8 fold. tables, 2 maps. [This is the author's German translation of the 1917 article.]
1925. Die Artenzahl als pflanzengeographischer Charakter, sowie der Zufall und die säkulare Landhebung als pflanzengeographische Faktoren. Ein pflanzengeographischer Entwurf, basiert auf Material aus dem Ålandischen Schärenarchipel. Acta Bot. Fenn. 1 (1): 1–42, 2 maps.

PETERSEN, C. G. JOH., and JENSEN, P. BOYSEN
1911. Valuation of the sea. I. Animal life of the seabottom, its food and quantity. (Quantitative studies). 78 + 3 pp., 6 tables, 3 charts, 6 pls. Rept. Danish Biol. Sta. 20. Copenhagen.

POTZGER, J. E.
1935. Topography and forest types in a central Indiana region. Am. Midl. Nat. 16: 212–229.
1946. Phytosociology of the primeval forest in central-northern Wisconsin and Upper Michigan, and a brief post-glacial history of the Lake Forest formation. Ecol. Monogr. 16: 211–250.

POTZGER, J. E., and FRIESNER, RAY C.
1940. What is climax in central Indiana? A five-mile quadrat study. Butler Univ. Bot. Studies 4: 181–195.

Potzger, J. E., Friesner, Ray C., and Keller, C. O.
1942. Phytosociology of the Cox Woods: a remnant of forest primeval in Orange County, Indiana. Butler Univ. Bot. Studies 5: 190–221.

Preston, F. W.
1948. The commonness, and the rarity, of species. Ecology 29: 254–283.

Ramaley, Francis
1914. The amount of bare ground in some mountain grasslands. Bot. Gaz. 57: 526–528.
1915. The relative importance of different species in a mountain grassland. Bot. Gaz. 60: 154–157.
1916. Quadrat studies in a mountain grassland. Bot. Gaz. 62: 70–74.
1942. Vegetation of the San Luis Valley in southern Colorado. Univ. Colo. Studies, Ser. D, 1 (4): 231–277.

Raunkiaer, C.
1910. Formationsundersøgelse og Formationsstatistik. Bot. Tidsskr. 30: 20–132. [Hefte 1, to p. 80, was issued Dec. 1909; vol. completed in 1910.]
1916. Om Bladstørrelsens Anvendelse i den biologiske Plantegeografi. Bot. Tidsskr. 34: 225–239.

Regel, Konstantin
1921. Statistische und physiognomische Studien an Wiesen. Acta Comment. Univ. Dorpat. (Tartu), Ser. A, 1 (4): 1–88.
1923. Die Pflanzendecke der Halbinsel Kola. I. Lapponia Varsugae. Mem. Faculté Sci. Univ. Lithuanie I. (1922). 24 + 246 pp. Kaunas.

Richards, P. W.
1933. (See Davis and Richards.)
1934.
1936. Ecological observations on the rain forest of Mount Dulit, Sarawak. Jour. Ecol. 24: 1–37, 340–360.
1939. Ecological studies on the rain forest of southern Nigeria. I. The structure and floristic composition of the primary forest. Jour. Ecol. 27: 1–61.
1945. The floristic composition of primary tropical rain forest. Biol. Rev. Cambridge Phil. Soc. 20 (1): 1–13.

Romell, Lars-Gunnar
1920. Sur la règle de distribution des fréquences. Svensk Bot. Tidskr. 14: 1–20.
1923. Till frågan om frekvensfördelningsregelns tolkning. Svensk Bot. Tidskr. 17: 231–240.
1925. Om inverkan av växtsamhällenas struktur pa växtsamhällsstatiskens resultat.—Résumé: L'influence de la structure des groupements végétaux sur les relevés de la statistique phytosociologique. Bot. Notiser 1925: 253–298, 299–308.
1926. Bemerkungen zum Homogenitäts problem. Svensk Bot. Tidskr. 20: 441–455.
1930. Comments on Raunkiaer's and similar methods of vegetation analysis and the "law of frequency". Ecology 11: 589–596.

Shantz, H. L., and Piemeisel, R. L.
1924. Indicator significance of the natural vegetation of the southwestern desert region. Jour. Agr. Research 28: 721–801, pls. 1–14.

Short, C. W.
1845. Observations on the botany of Illinois, more especially in reference to the autumnal flora of the prairies. West. Jour. Med. & Surgery, New Ser., 3: 185–198.

Shreve, Forest
1942. The desert vegetation of North America. Bot. Rev. 8: 195–245.

Sobrinho, Vasconcellos
1937. Estudos e observações sobre as mattos de Pernambuco. Fronteiras, No. 23. 40 pp., 9 pls. Feb. 1937.—Abstract by B. E. DAHLGREN in Tropical Woods No. 52: 37–38. 1937.

Steiger, T. L.
1930. Structure of prairie vegetation. Ecology 11: 170–217.

Svedberg, The
1922a. Ett bidrag till de statistika metodernas användning inom växtbiologien. Svensk Bot. Tidskr. 16: 1–8.
1922b. Statistik vegetationsanalys. Svensk. Bot. Tidskr. 16: 197–205.

Teräsvuori, Kaarlo
1927. Wiesenuntersuchungen, II. Ann. Soc. Zool. Bot. Fenn. Vanamo 7 (3): 311–392.

Thompson, David H., and Hunt, Francis D.
1930. The fishes of Champaign County. A study of the distribution and abundance of fishes in small streams. Ill. Nat. Hist. Surv., Bull. 19 (1): 1–101, 52 maps.

Thornber, John J.
1901. The prairie-grass formation in Region I. Univ. Nebr., Bot. Surv. Nebr. 5: 29–143.

Vahl, Martin
1911. Les types biologiques dans quelques formations végétales de la Scandinavia. Oversigt Kgl. Danske Videnskabernes Selskabs Forhandlinger 1911: 319–393.
1913. The growth-forms of some plant formations of Swedish Lapland. Dansk. Bot. Arkiv 1 (2): 1–18.

Van der Laan, E.
1926. [Forest statistics, southeast Borneo: Tanah Boemboe and Pleihari.] Tectona 19: 103–, 215–.—Cited by MILDBRAED, 1930a.
1927. De analyse der bosschen van de eilanden Poeloe Laoet en Seboekoe der Residentie Zuideren Oosterafdeeling van Borneo. Tectona 20: 19–36.—Cited by MILDBRAED. Title from Internat. Rev. Agric.

Vaughan, R. E., and Wiehe, P. O.
1941. Studies on the vegetation of Mauritius. III. The structure and development of the upland climax forest. Jour. Ecol. 29: 127–160.

Vestal, Arthur G.
1913. A black-soil prairie station in northeastern Illinois. Bull. Torr. Bot. Club 41: 351–363.
1914. Prairie vegetation of a mountain-front area in Colorado. Bot. Gaz. 58: 377–400.
1917. Foothills vegetation in the Colorado Front Range. Bot. Gaz. 64: 353–385.

1919. Phytogeography of the eastern mountain-front in Colorado. Bot. Gaz. 68: 153–193.

1946a. Minimum extent of associations and stands. Bull. Ecol. Soc. Am. 27 (1): 15. (Abstract.)

1946b. Determination of minimum areas on species-area curves. Bull. Ecol. Soc. Am. 27 (1): 15. (Abstract.)

VESTAL, ARTHUR G., and HEERMANS, MARY FRANCES

1945. Size requirements for reference areas in mixed forest. Ecology 26: 122–134.

WARMING, EUG.

1899. On the vegetation of tropical America. Bot. Gaz. 27: 1–18.

WHITFORD, HARRY NICHOLS

1906. The vegetation of the Lamao Forest Reserve. Phil. Jour. Sci. 1: 373–431, 637–682; pls. 1–45, map.

1909. The composition and volume of the dipterocarp forests of the Philippines. Phil. Jour. Sci. 4 (C): 699–725, pls. 32–38.

1911. The forests of the Philippines. Bull. P. I. Bur. Forestry No. 10. Vol. I. Forest types and products. 94 pp., 28 pls., map. Vol. II. the principal forest trees. 113 pp., 103 pls.

WICKSELL, S. D.

1924. Några formella synpunkter beträffande fördelningskurvorna inom växtsociologen. Bot. Notiser 1924: 17–37.

WILLIAMS, C. B.

1944. Some applications of the logarithmic series and the index of diversity to ecological problems. Jour. Ecol. 32: 1–44.—See FISHER, CORBET, and WILLIAMS, 1943.

WILLIS, J. C.

1940. The course of evolution by differentiation or divergent mutation rather than by selection. 207 pp. Cambridge Univ. Press. Chap. 4. The hollow curve, pp. 33–42.—Review by SEWALL WRIGHT, Ecology 22: 345–347.

WILLIS, J. C., and YULE, G. UDNY

1922. Some statistics of evolution and geographic distribution in plants and animals, and their significance. Nature 109: 177–179.

WOOLLETT, E., DEAN, D., and COBURN, H.

1925. Application of Gleason's formula to a Carex lasiocarpa association, an association of few species. Bull. Torr. Bot. Club. 52: 23–25.

ZIEGLER, E. A.

1904. Natural timber of northern and central Illinois. MS., U. S. Forest Service. [This MS was made available by the Forest Service, with the helpful mediation of Richard J. Costley.]

ILLINOIS BIOLOGICAL MONOGRAPHS

(Continued from inside front cover)

Vol. VII

No. 1. Studies on Gregarines, II. Synopsis of the Polycystid Gregarines. With 4 plates. By Minnie Watson Kamm. $1.00.

No. 2. The Molluscan Fauna of the Big Vermilion River, Illinois. With 15 plates. By F. C. Baker. $1.25.

No. 3. North American Monostomes. With 9 plates. By E. C. Harrah. $1.25.

No. 4. A Classification of the Larvae of the Tenthredinoidea. With 14 plates. By H. Yuasa. $2.00.

Vol. VIII

No. 1. The Head-capsule of Coleoptera. With 26 plates. By F. S. Stickney. $2.00.

No. 2. Comparative Studies on Certain Features of Nematodes and Their Significance. With 4 plates. By D. C. Hetherington. $1.00.

No. 3. Parasitic Fungi from British Guiana and Trinidad. With 19 plates. By F. L. Stevens. $1.25.

No. 4. The External Morphology and Postembryology of Noctuid Larvae. With 8 plates. By L. B. Ripley. $1.25.

Vol. IX

No. 1. The Calciferous Glands of Lumbricidae and Diplocardia. With 12 plates. By Frank Smith. $1.25.

Nos. 2-3. A Biologic and Taxonomic Study of the Microsporidia. With 27 plates and 9 text-figures. By R. Kudo. $3.00.

No. 4. Animal Ecology of an Illinois Elm-maple Forest. With 7 plates. By A. O. Weese. $1.25.

Vol. X

No. 1. Studies on the Avian Species of the Cestode Family Hymenolepididae. With 9 plates and 2 text-figures. By R. L. Mayhew. $1.50.

No. 2. Some North American Fish Trematodes. With 6 plates, 2 charts, and 1 text-figure. By H. W. Manter. $1.50.

No. 3. Comparative Studies on Furcocercous Cercarie. With 8 plates and 2 text-figures. By H. M. Miller. $1.25.

No. 4. A Comparison of the Animal Communities of Coniferous and Deciduous Forests. With 16 plates. By I. H. Blake. $1.50.

Vol. XI

No. 1. An Ecological Study of Southern Wisconsin Fishes. With 16 plates. By A. R. Cahn. $1.50.

No. 2. Fungi from Costa Rica and Panama. With 18 plates. By F. L. Stevens. $1.25.

No. 3. The Structure and Development of Corallobothrium. With 5 plates. By H. E. Essex. $1.00.

No. 4. Caryophyllaeidae of North America. With 7 plates. By G. W. Hunter, III. $1.25.

Vol. XII

No. 1. Morphological Studies of the Genus Cercospora. With 4 plates. By W. G. Solheim. $1.00.

No. 2. Morphology, Taxonomy, and Biology of Larval Scarabaeoidea. With 15 plates. By W. P. Hayes. $1.25.

No. 3. Sawflies of the Sub-family Dolerinae of America North of Mexico. With 6 plates. By H. H. Ross. $1.25.

No. 4. A Study of Fresh-water Plankton Communities. By Samuel Eddy. $1.00.

Vol. XIII

No. 1. Studies on Some Protozoan Parasites of Fishes of Illinois. With 8 plates. By R. R. Kudo. 75 cts.

No. 2. The Papillose Allocreadiidae: A Study of Their Morphology, Life Histories, and Relationships. With 4 plates and 6 text-figures. By S. H. Hopkins. $1.00.

No. 3. Evolution of Foliar Types, Dwarf Shoots, and Cone Scales of Pinus. With 32 text-figures. By C. C. Doak. $1.50.

No. 4. A Monographic Rearrangement of Lophodermium. With 5 plates. By L. R. Tehon. $2.00.

[*Continued on back cover.*]

ILLINOIS BIOLOGICAL MONOGRAPHS

(Continued from inside back cover)

Vol. XIV

No. 1. Development of the Pectoral Limb of *Necturus maculosus*. With 11 plates. By H. K. Chen. $1.00.

No. 2. Studies on North American Cercariae. With 8 plates. By E. L. Miller. $1.50.

No. 3. Studies on the Morphology and Life History of Nematodes in the Genus Spironoura. With 5 plates and 2 text-figures. By J. G. Mackin. $1.00.

No. 4. The Life History of *Cotylophoron cotylophorum*, a Trematode from Ruminants. With 9 plates. By H. J. Bennett. $1.50.

Vol. XV

No. 1. Experimental Studies on *Echinostoma revolutum* (Froelich), a Fluke from Birds and Mammals. With 3 plates. By P. C. Beaver. $1.00.

No. 2. Generic Classification of Nearctic Sawflies. With 17 plates. By H. H. Ross. $2.00.

No. 3. Studies on the Biology of the Crayfish *Cambarus propinquus* Girard. With 46 graphs. By W. C. Van Deventer. $1.00.

No. 4. Taxonomic Studies on the Mouth Parts of Larval Anura. With 3 figures and 8 charts. By R. J. Nichols. $1.00.

Vol. XVI

Nos. 1-2. The Turtles of Illinois. With 31 plates, 20 maps, and 15 text-figures. By A. R. Cahn. $3.00.

No. 3. The Phylogeny of the Hemiptera, Based on a Study of the Head Capsule. With 24 plates. By C. S. Spooner. $1.00.

No. 4. A Classification of the Larvae and Puparia of the Syrphidae of Illinois. Exclusive of Aquatic Forms. With 17 plates. By Elizabeth M. Heiss. $1.50.

Vol. XVII

No. 1. Comparative Studies on Trematodes (Gyrodactyloidea) from the Gills of North American Fresh-water Fishes. With 5 plates. By J. D. Mizelle. $1.00.

No. 2. The Microthyriaceae. By F. L. Stevens and Sister M. Hilaire Ryan. $1.50.

No. 3. The Branchiobdellidae (Oligochaeta) of North American Crayfishes. With 3 plates. By C. J. Goodnight. $1.00.

No. 4. Cytological Observations on *Endamoeba blattae*. With 8 plates. By P. A. Meglitsch. $1.00.

Vol. XVIII

No. 1. Generic Relationships of the Dolichopodidae (Diptera) Based on a Study of the Mouth Parts. With 30 plates. By Sister Mary Bertha Cregan. $1.00.

No. 2. Studies on *Gregarina blattarum* with Particular Reference to the Chromosome Cycle. With 6 plates and 2 text-figures. By Victor Sprague. 75 cts.

No. 3. Territorial and Mating Behavior of the House Wren. With 32 figures. By S. C. Kendeigh. $1.50.

No. 4. The Morphology, Taxonomy, and Bionomics of the Nemertean Genus Carcinonemertes. With 4 plates and 1 map. By A. G. Humes. $1.50.

Vol. XIX

Nos. 1-2. The Ostracods of Illinois—Their Biology and Taxonomy. With 9 plates. By C. C. Hoff. 2.50.

No. 3. The Genus Conotrachelus Dejean (Coleoptera, Curculionidae) in the North Central United States. With 9 plates. By H. F. Schoof. $1.50.

No. 4. The Embryology of Larix. With 86 figures. By J. M. Schopf. $1.50.

Vol. XX

No. 1. Morphology and Development of *Nosema notabilis* Kudo, Parasitic in *Sphaerospora polymorpha* Davis, a Parasite of *Opsanus tau* and *O. beta*. With 12 plates and 7 text-figures. By R. R. Kudo. $1.25.

No. 2. American Species of Amelanchier. With 23 plates and 14 maps. By G. N. Jones. $1.50.

UNIVERSITY OF ILLINOIS-URBANA
3 0112 083213048